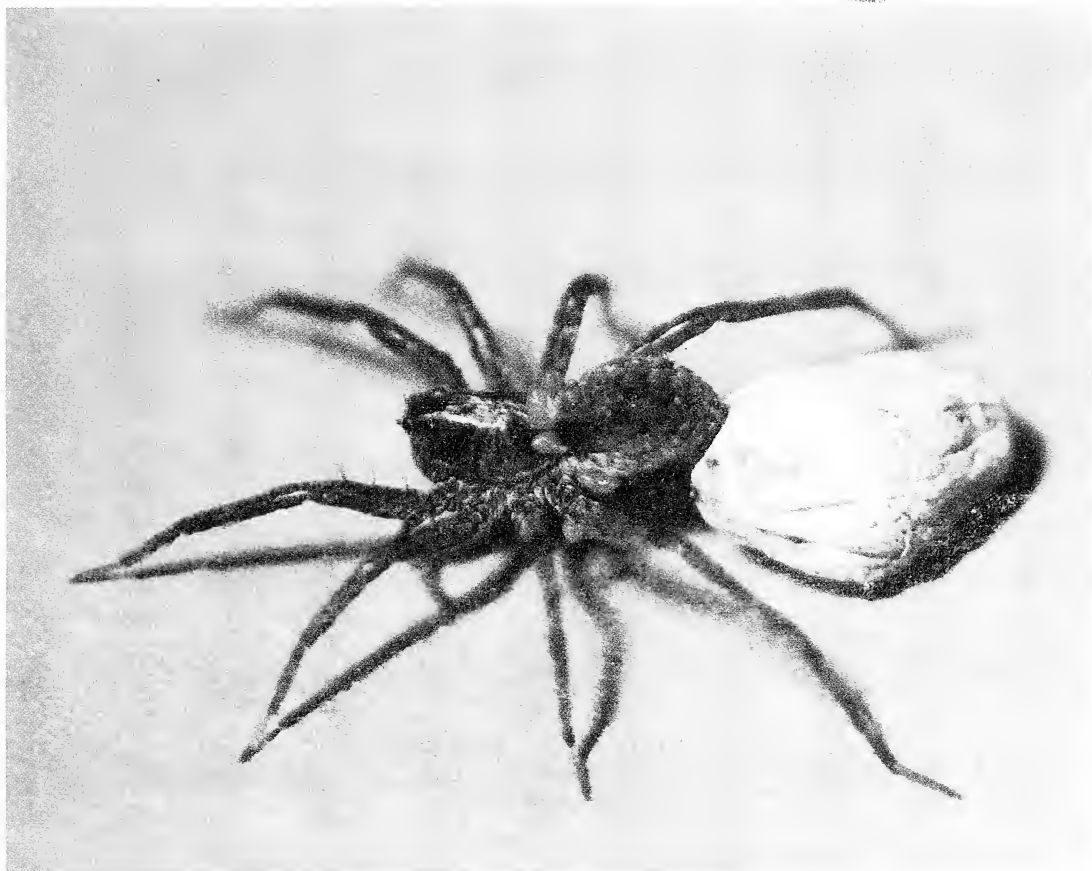
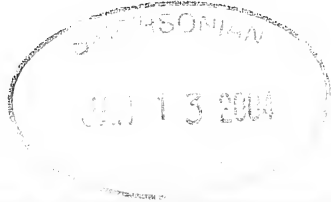


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Cover photo: *Trochosa terricola* Thorell 1856 from Dutchess County, New York with mites around anterior of abdomen. Egg sac with a dipterous parasite. Photo by Gail Stratton., Oxford, MS.

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THE GENUS *BRACHISTOSTERNUS* IN ARGENTINA, WITH A DESCRIPTION OF A NEW PATAGONIAN SPECIES (SCORPIONES, BOTHRIURIDAE)

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ABSTRACT. The new species *Brachistosternus paulae* is described. This is the southernmost species of the genus, occurring in southern Patagonia in Santa Cruz Province. It can be distinguished from all the other species of the genus by the presence of only 4 ventral trichobothria on the pedipalpal chela, and by the shape of the hemispermatophore, in which the cylindrical apophysis is shorter than the laminar apophysis; all internal spines are absent, except for the row of spines, which in some specimens is vestigial. This species can not be included in any of the known subgenera due to its trichobothrial pattern; nevertheless it is closer to the subgenus *Leptosternus* on the basis of its remaining morphology. A key for the species of the genus in the country is provided together with some data on them. The hemispermatophores of the three subgenera are compared and two maps detailing the distribution of the species in the country are provided.

El género *Brachistosternus* en la Argentina, con la descripción de una nueva especie de la Patagonia (Scorpiones, Bothriuridae). En este trabajo se describe a *Brachistosternus paulae* n. sp. Esta es la especie conocida más austral del género, habitando en el sur de la Patagonia en la provincia de Santa Cruz. Puede diferenciarse del resto de las especies del género por la presencia de solo 4 tricobotrias ventrales en la pinza y por el escaso desarrollo de su hemispermatóforo, en éste la apófisis cilíndrica se encuentra poco desarrollada y es más corta que la apófisis laminar, además carece de todos los procesos espiniformes, salvo las espinas en hilera que en algunos ejemplares pueden presentarse en forma vestigial; la particular tricobotriotaxia de esta especie no permite incluirla en ninguno de los subgéneros descritos hasta el momento, sin embargo su morfología la aproxima más al subgénero *Leptosternus*. Se presenta además una clave para las especies del género en el país y se aportan algunos datos sobre éstas. Se comparan los hemispermatóforos de los distintos subgéneros y se presentan dos mapas con la distribución de las distintas especies presentes en el país.

Keywords: Scorpiones, *Brachistosternus*, key, new species, Argentina

Within Argentina, the genus *Brachistosternus* Pocock 1893 is a dominant component of the scorpion fauna in the arid and semiarid areas that occupy more than half of the national territory. It can be found from sea level up to more than 4000 m a.s.l.. Although the Argentinian scorpion fauna has been well studied, relatively few works have been published on this genus: Roig Alsina (1977), Maury (1973, 1974, 1975, 1978a, 1978b, 1984), Roig Alsina & Maury (1981, 1984), Prendini (2000), San Martín (1969), Ojanguren Affilastro (2000, 2001, 2002) and Ojanguren Affilastro & Roig Alsina (2001).

This genus presents a high degree of intra-specific variability, especially in the species of

the subgenus *Leptosternus* Maury 1973. For this reason, it is sometimes necessary to study large numbers of specimens to define a species clearly. Intraspecific variability is shown by color, external morphological structures or the structures of the hemispermatophore, and it may be intrapopulational or interpopulational.

An interesting characteristic of the genus *Brachistosternus* is the complexity of its hemispermatophore, which has a basic pattern in the three subgenera. Nevertheless, there are important differences in the internal structures of the lobe region. A comparison of the hemispermatophores of the three subgenera is herein presented.

There are no modern keys for the species of the genus. The last one was provided by Mello Leitão (1945). A key and a catalogue for the known species of the genus *Brachistosternus* from Argentina is herein presented. The characters that are more often used in the taxonomy of this genus are the structures of the hemispermatophore, the trichobothrial pattern, the number of metasomal and tarsal setae, morphometric ratios and the particular morphological characteristics of the different species, such as the granulation of the telson or the shape of the telotarsi.

In this work, *Brachistosternus paulae*, the southernmost species of the genus, is described. Its particular trichobothrial pattern prevents it from being included in any of the known subgenera of the genus. Maps of the distribution of the Argentinian species of *Brachistosternus* have been prepared based upon all localities cited by the bibliography of the present catalogue, except for the localities of *B. paulae*.

METHODS

Terminology of the structures of the hemispermatophore follows Maury (1974). Trichobothrial terminology follows Vachon (1974). Terminology of the androvestigia follows Cekalovic (1973). Terminology of the telson gland follows Roig Alsina & Maury (1981). Terminology of the metasomal carinae follows Stahnke (1970). Terminology of the metasomal ventral setae follows Ojanguren Affilastro & Roig Alsina (2001). Terminology of the Phytogeographic Provinces follows Cabrera & Willink (1980). Terminology of the Scorpioneological Areas follows Acosta & Maury (1998). Abbreviations are as follows: MACN-Ar = Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", National Arachnological Collection (Cristina Scioscia); a.s.l. = above sea level; NMW = Naturhistorisches Museum Wien, Vienna, Austria; MIZT = Museo ed Instituto di Zoologia sistematica della Università, Turin, Italy; MNHN = Museum National D'Histoire Naturelle, Paris, France; NRS = Naturhistoriska Riksmuseet, Stockholm, Sweden; ZMH = Zoologische Staatinstitut, Zoologisches Museum, Hamburg, Germany; NMB = Naturhistorisches Museum, Basel, Switzerland. All measurements are in mm, and were taken using an ocular micrometer. Illustrations were produced using a

stereomicroscope and camera lucida. The hemispermatophores were dissected from surrounding tissues and observed in 80% ethanol.

RESULTS

CATALOGUE OF THE ARGENTINIAN SPECIES OF *BRACHISTOSTERNUS*

Brachistosternus (*Brachistosternus*) *ehrenbergii* (Gervais 1841)

Scorpio ehrenbergii Gervais 1841:282–283, figs. 18–22, pl. I. (Holotype male, Callao, Peru (ZMH), not examined).

Scorpio glaber Gervais, 1841:285, figs. 28–32, pl. I (synonymized by Simon, 1880:397). (Holotype, Peru (MNHN), not examined).

Telogonus politus Koch, 1867:234–235 (synonymized by Kraepelin, 1894:216). (Holotype female, South America (ZMH), not examined).

Remarks.—This is the type species of the genus. It has been collected from Ecuador to Chile, but the presence of this species in Argentina is dubious (Fig. 28) (Maury 1973).

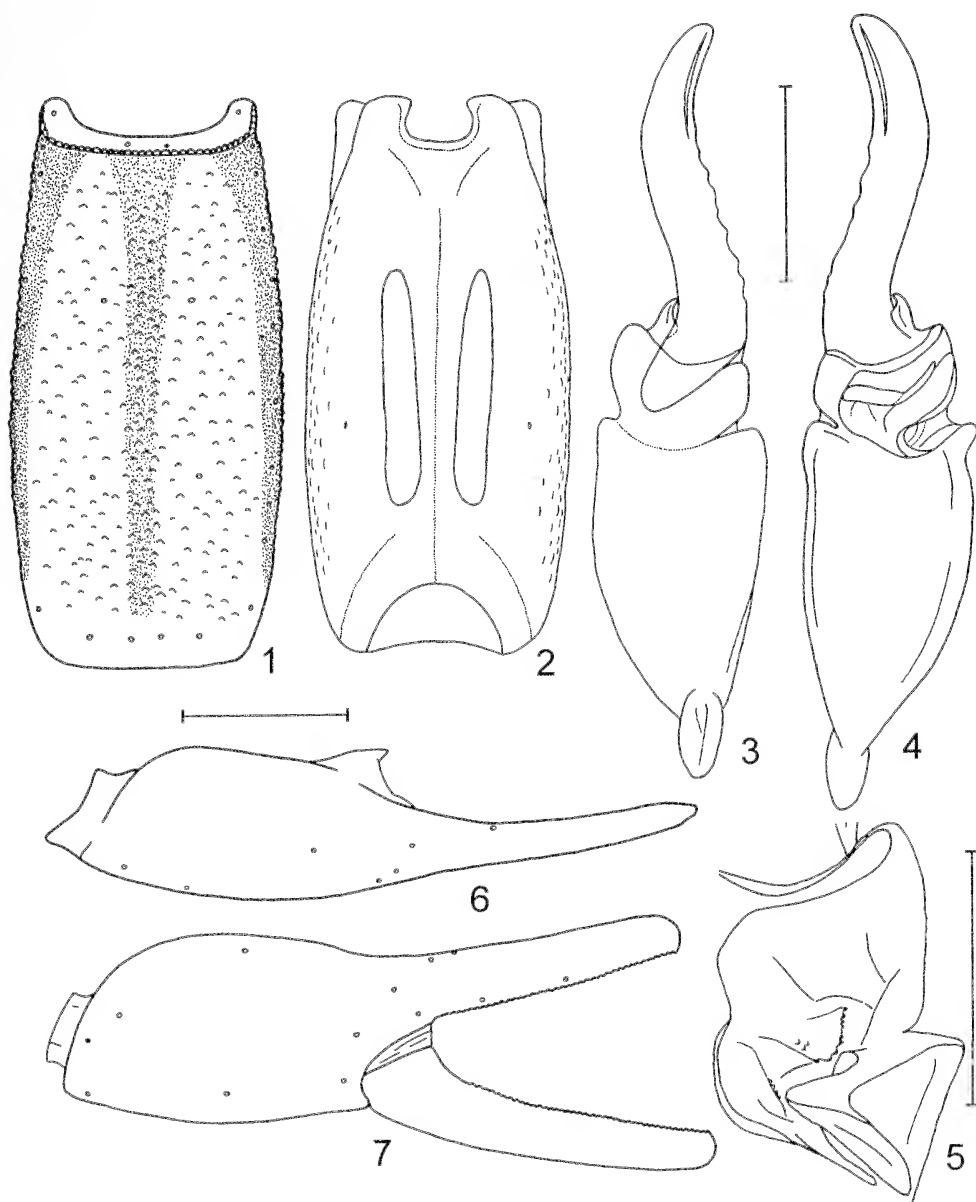
Brachistosternus (*Leptosternus*) *alienus* Lönnberg 1898

Brachistosternus alienus Lönnberg 1898:46–48. (Holotype female, Puerto Madryn, Chubut Province, Argentina (NRS), not examined).

Remarks.—*Brachistosternus alienus* is endemic to southern Argentina (Fig. 28). It has been collected in southern "Monte" Phytogeographic Province, and Northern "Patagonia" Phytogeographic Province; from sea level up to 1000 m a.s.l. (Ojanguren Affilastro 2001). Cekalovic (1966, 1983) reported this species from Chile, but its presence in this country is unlikely. This species was found in sympatry with *Bothriurus burmeisteri* Kraepelin 1894; *Zabius birabeni* Mello Leitão 1938; *Timogenes elegans* (Mello Leitão 1931); *Brachistosternus pentheri* Mello Leitão 1931 and *B. angustimanus* Ojanguren Affilastro & Roig Alsina 2001.

Brachistosternus (*Leptosternus*) *angustimanus* Ojanguren Affilastro & Roig Alsina 2001

Brachistosternus (*Leptosternus*) *angustimanus* Ojanguren Affilastro & Roig Alsina 2001: 16–22, 1–14, 17, tab. I, II. (Holotype male, Las Grutas, Rio Negro Province, Argentina (MACN-Ar 9732)).



Figures 1–7.—*Brachistosternus paulae* new species: 1. Fifth metasomal segment, ventral aspect; 2. Fifth metasomal segment, male, dorsal aspect; 3. Left hemispermatophore, dorsal aspect; 4. Left hemispermatophore, ventral aspect; 5. Left hemispermatophore, detail of the lobe region; 6. Right pedipalp chela, male, dorsal aspect; 7. Right pedipalp chela, female, retrolateral aspect. Scale bars = 1 mm.

Remarks.—This species is endemic to southern Argentina (Fig. 29), from sea level up to 1000 m a.s.l. (Ojanguren Affilastro & Roig Alsina 2001). It has been previously confused with *B. (L.) alienus* by several authors (Mello Leitão 1938; Maury 1973; Ringuelet 1953).

Most of the species of the genus *Brachis-*

tosternus are not found in sympatry with other congeners; when they inhabit the same region they are usually in parapatry, at different elevations or in different environments. However the distributions of *B. (L.) alienus* and *B. (L.) angustimanus* overlap almost entirely (Ojanguren Affilastro & Roig Alsina 2001). *Brachistosternus angustimanus* was also

found in sympatry with *Bothriurus burmeisteri*, *Zabius birabeni* and *Timogenes elegans*.

Brachistosternus (Leptosternus) intermedius Lönnberg 1902

Brachistosternus weijenberghi intermedia Lönnberg 1902:255. (Two juvenile syntypes, Ojo de Agua, Salta Province, Argentina (NRS), not examined).

Remarks.—This species occurs between 2500 and 4000 m a.s.l., from northwestern Argentina to southwestern Bolivia (Fig. 29). It was found in sympatry with *Bothriurus olaen* Acosta 1997. The specimens of *Brachistosternus (Leptosternus) castroi* Mello Leitão 1940 mentioned from Argentina (Ringuelet 1953), actually belong to *B. (L.) intermedius* Lönnberg (Ojanguren Affilastro in press b).

Brachistosternus (Leptosternus) montanus Roig Alsina 1977

Brachistosternus (Leptosternus) montanus Roig Alsina 1977:255–259, figs. 1–7. (Holotype male, Puente del Inca, Mendoza Province, Argentina (MACN-Ar 7060), examined)

Remarks.—*Brachistosternus (L.) montanus*, a closely related species to *B. (L.) intermedius* Lönnberg (Ojanguren Affilastro in press b), occurs at the same altitudes but in the center of the country (Fig. 29), in the Provinces of San Juan and Mendoza (Roig Alsina 1977; Roig Alsina & Maury 1981). It was found in sympatry with *Orobothriurus alticola* (Pocock 1899) (Roig Alsina 1977; Roig Alsina & Maury 1981).

Brachistosternus (Leptosternus) multidentatus Maury 1984

Brachistosternus (Leptosternus) multidentatus Maury 1984:113–116, figs. 1–7, tab. I. (Holotype male, Bermejo, Caucete department, San Juan Province, Argentina (MACN-Ar 7849), examined).

Remarks.—This is a psammophilic species that has a disjunct distribution in the Provinces of San Juan and Buenos Aires (Fig. 28). It occurs in dunes without vegetation. In dunes with some vegetation, it is replaced by *Brachistosternus pentheri* Mello Leitão 1931 (Maury 1984). *Brachistosternus multidentatus* has been collected in sympatry with *Vachonia martinezi* Abalos 1954, in southern Buenos Aires. This species has the highest number of pectinal teeth of the genus, the females have

38–44 pectinal teeth and the males 45–58 (Maury 1984).

Brachistosternus (Leptosternus) pentheri Mello Leitão 1931

Brachistosternus pentheri Mello Leitão 1931:94, 95. (Holotype male, Arístides Villanueva Department, Mendoza Province, Argentina (NMW), not examined).

Brachistosternus (Leptosternus) psammophilus Maury 1978a:169–175, fig. 1–9, tab. I–IV (synonymized by Roig Alsina & Maury 1984:18). (Holotype male, Sauce Grande, Coronel Dorrego, Buenos Aires Province, Argentina (MACN-Ar 7026), examined).

Remarks.—This species was reviewed by Roig Alsina & Maury (1984). It is endemic to central and northern Argentina, from sea level up to 1500 m a.s.l.; from Buenos Aires Province to Jujuy Province (Roig Alsina & Maury 1984) (Fig. 29). It was found in sympatry with: *Bothriurus burmeisteri*, *B. prospicius* Mello Leitão 1934, *B. cordubensis* Acosta 1995, *B. chacoensis* Maury & Acosta 1993, *Zabius birabeni*, *Z. fuscus* (Thorell 1877), *Timogenes elegans*, *T. dorbignyi* (Guérin & Meneville 1843), *Vachonia* sp., *Brachistosternus alienus*, *B. weyenberghii* (Thorell 1876), *B. ferrugineus* (Thorell 1876), *B. telteca* Ojanguren Affilastro 2000, *Tityus trivittatus* Kraepelin 1898 and *T. confluentis* Borelli 1899 (Acosta 1995).

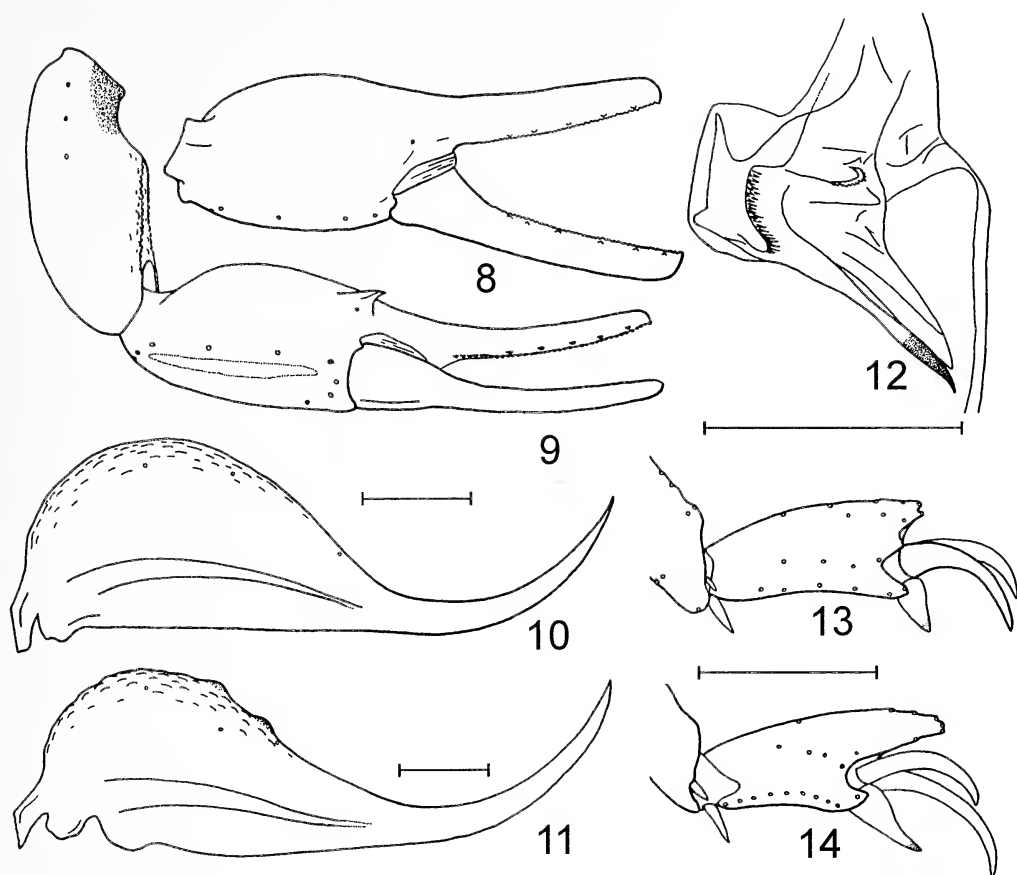
Brachistosternus (Leptosternus) weyenberghii (Thorell 1876)

Teloganus weijenberghii Thorell 1876:173–176. (Holotype male, Cordova, Argentina (NRS), not examined).

Brachistosternus weijenberghi reimoseri Penther 1913:247–248 (synonymized by Ojanguren Affilastro in press a). (Holotype juvenile female, Mendoza, Argentina (NMW), not examined).

Brachistosternus intermedius borellii Kraepelin 1911:86 (synonymized by Ojanguren Affilastro in press a). (Holotype female, Cacheuta, Mendoza, Argentina (MIZT), not examined).

Remarks.—*Brachistosternus borellii* Kraepelin 1911 and *B. weijenberghii reimoseri* Penther 1913 are junior synonyms of *B. weyenberghii* (Thorell 1876) (Ojanguren Affilastro in press a), which occurs between 900 and 2900 m a.s.l., in the center and northwestern areas of Argentina (Ojanguren Affilastro in press a) (Fig. 28). This species demonstrates clinal variation of the length of the distal lam-



Figures 8–14.—8–10. *Brachistosternus paulae* new species: 8. Left pedipalp chela, female, prolateral aspect; 9. Left pedipalp chela and patella, male, ventral aspect; 10. Telson, male, lateral aspect; 11. *Brachistosternus* (L.) *weyenbergii*, telson, male, lateral aspect; 12. *Brachistosternus* (L.) *intermedius*, left hemispermatophore, detail of the lobe region; 13. *Brachistosternus* (L.) *penteri*, telotarsus IV, lateral aspect; 14. *Brachistosternus* (L.) *multidentatus*, telotarsus IV, lateral aspect. Scale bars = 1 mm.

ina of the hemispermatophore, with the one in the northern populations being longer than the one in southern populations.

Roig Alsina & Maury (1984) reviewed *B. borellii* and observed and described for the first time, a kidney shaped gland on the dorsal face of the telson. This gland does not correspond to the androvestigia described by Cechalovic (1973). Recently this kidney shaped gland was found in other species of the genus (Ojanguren Affilastro 2001).

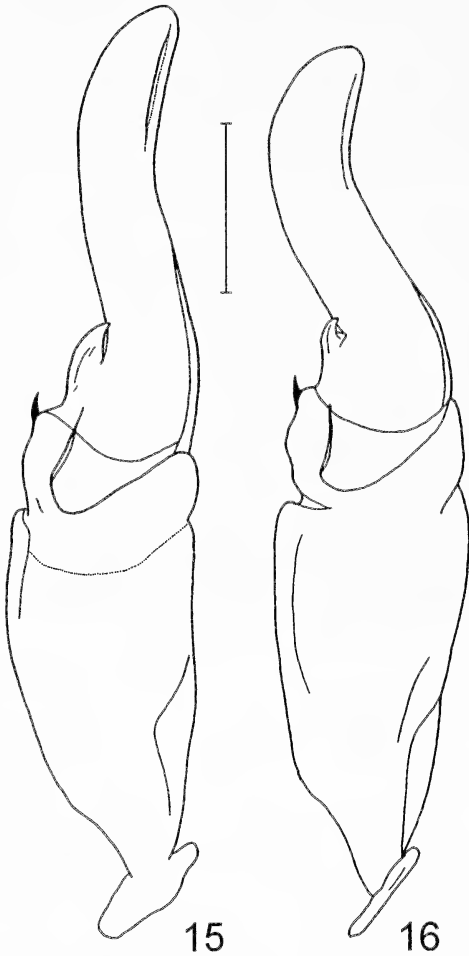
This species has never been collected again in its type locality in Cordoba Province (Acosta & Rosso de Ferradás 1996). It was found in sympatry with *Bothriurus burmeisteri*, *B. olaen* and *Brachistosternus zambrunoi* Ojanguren Affilastro 2002. An isolated population of this species from southern La Rioja is also

in sympatry with *Zabius fuscus*, *Timogenes elegans*, *T. dorbignyi*, *Bothriurus cordubensis* Acosta 1995, *Tityus confluens*, *Brachistosternus penteri* and *B. ferrugineus* (Mattoni & Acosta 1997).

In this work the specific epithet *weyenbergii* is used following Fet, Sissom, Lowe & Braunwalder (2000), but the actual spelling of the surname of the scientist in honor of whom this species was named was Weijenbergh, not Weyenbergh (Dr. A. O. Bachmann pers. comm.).

Brachistosternus (*Leptosternus*) *zambrunoi*
Ojanguren Affilastro 2002

Brachistosternus (*Leptosternus*) *zambrunoi* Ojanguren Affilastro 2002:33–38, figs. 1–8, 15–19, tab. I. (Holotype male: El Arenal, Catamarca Province, Argentina (MACN-Ar 10206)).



Figures 15–16.—15. *Brachistosternus* (L.) *zambrunoi*, left hemispermatophore, dorsal aspect. 16. *Brachistosternus* (L.) *intermedius*, left hemispermatophore, dorsal aspect. Scale bar = 1 mm.

Remarks.—This is a psammophilic species that occurs in a small area in northern Catamarca and southern Salta, between 1500 and 2000 m a.s.l. (Fig. 29). It was found in sympatry with *Brachistosternus weyenberghii*, *Bothriurus olaen* and *Timogenes elegans* (Ojanguren Affilastro 2002).

Brachistosternus (Ministernus) *ferrugineus* (Thorell 1876)

Telogonus ferrugineus Thorell 1876:176, 177. (Holotype female, “Cordova”, Argentina (NRS), not examined).

Brachistosternus andinus reichlini Schenkel 1949: 197–201, figs. 4a, 4c (synonymized by Maury, 1974:75). (Holotype female: Rio “Saludo”, Chaco Province, Argentina (NMB), not examined).

Remarks.—This species was reviewed by Maury (1974). It was collected from central Argentina to southern Paraguay (Fig. 28); from the sea level up to 1000 m a.s.l. (Mattoni & Acosta 1997). This is probably the most common *Brachistosternus* of the “Chaqueña” Phytogeographic Province, but it also occurs at the “Monte” and “Espinal” Phytogeographic Provinces (Maury 1974). It was found in sympatry with *Bothriurus burmeisteri*, *B. prospicius*, *B. cordubensis*, *B. chacoensis*, *Zabius birabeni*, *Z. fuscus*, *Timogenes elegans*, *T. dorbignyi*, *Vachonia* sp., *Brachistosternus pentheri*, *B. weyenberghii*, *Tityus trivittatus* and *T. confluens* (Acosta 1995).

Brachistosternus holmbergi
Carbonell 1923

Brachistosternus holmbergi
Carbonell 1923:358, 359, fig. (Holotype male, Jujuy Province, Argentina (depository unknown)).

Remarks.—*Brachistosternus holmbergi* (whose type is lost) is considered a probable synonym of *B. (B.) ehrenbergii*. Although there are no specimens to confirm its presence in this country, this species occurs in Bolivia and Chile, and this is the only *Brachistosternus* of the region that matches the description of *B. holmbergi* (Maury 1973).

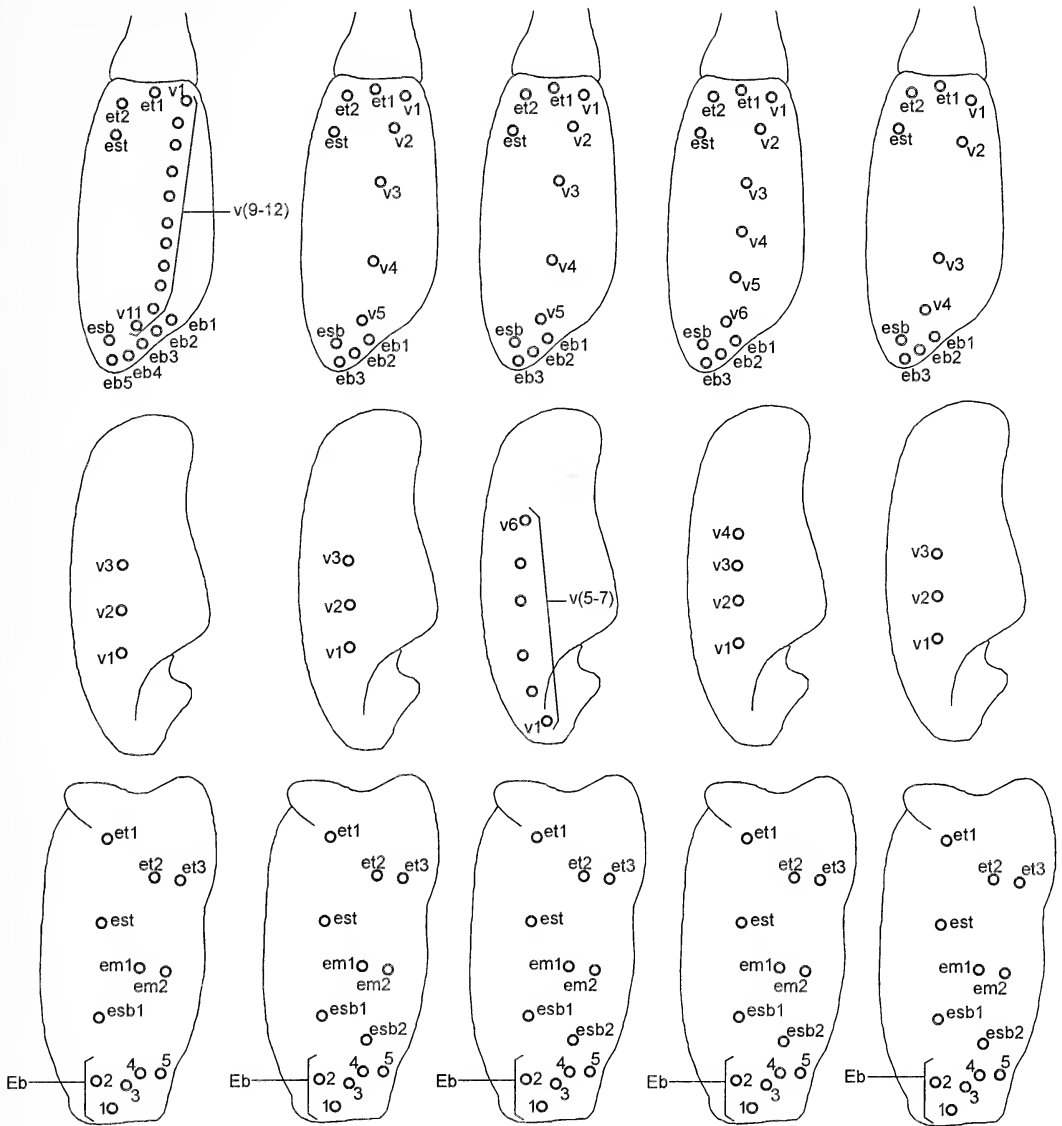
Brachistosternus telteca Ojanguren
Affilastro 2000

Brachistosternus telteca Ojanguren Affilastro 2000: 157–160, figs. 1–8, tab. I. (Holotype male, Reserva Telteca, Mendoza Province, Argentina (MACN-Ar 9931)).

Remarks.—This is a very rare psammophilic species that occurs in a small area in northern Mendoza Province (Ojanguren Affilastro 2000) (Fig. 28). It was found in sympatry with *Brachistosternus pentheri*, *Bothriurus burmeisteri* and *Timogenes elegans*. *Brachistosternus telteca* can not be included in any of the known subgenera because of its particular trichobothrial pattern (Fig. 20).

Brachistosternus paulae new species
(Figs. 1–10, 21, 29)

Type data.—Holotype male, Punta Peligro (46°44'S, 67°53'W), Santa Cruz Province, Argentina, 5 February 1978, Maury coll. (MACN-Ar 10082). Paratypes: ARGENTINA: Santa Cruz Province: 28 females, 24 males, 9 juveniles, Punta Peligro, 5 February



17. *B. (Ministernus)* 18. *B. (Leptosternus)* 19. *B. (Brachistosternus)* 20. *B. telteca* 21. *B. paulae*

Figures 17–21.—Trichobothrial pattern of genus *Brachistosternus*: chela, ventral aspect, patella ventral aspect and patella dorsal aspect; 17. subgenus *Ministernus*; 18. subgenus *Leptosternus*; 19. subgenus *Brachistosternus*; 20. *B. telteca*; 21. *B. paulae*.

1978, Maury coll. (MACN-Ar 10083); 9 females, 2 males, 4 juveniles, 11 January 1978, Maury coll. (MACN-Ar 10084); 8 females, 2 males, 21 January 1977, Maury coll. (MACN-Ar 10085).

Other specimens examined.—ARGENTINA: *Santa Cruz Province*: 1 ♀, 1 ♂, 1 juvenile, Lago Ghio (47°26'S, 70°56'W), 16 January 1978, Maury coll. (MACN-Ar 10086); 1 juvenile, Las Heras (46°32'S, 68°57'W), 18

January 1978, Maury coll. (MACN-Ar 10087).

Etymology.—This species is named after Paula Korob for her help in the field work

Diagnosis.—*Brachistosternus paulae* can be distinguished from the remaining species of the genus by having only 4 ventral trichobothria on the pedipalp chela. Its closest relative is *Brachistosternus (Leptosternus) alienus* Lönnberg 1898. Both species can be

distinguished, besides the trichobothrial pattern, by the different shape of their hemispermatophores. In *B. paulae* the cylindrical apophysis is poorly developed and shorter than the laminar apophysis (Fig. 5); it also lacks all spines, except for the row of spines that may be present in some specimens but in a vestigial form. In *B. alienus* the cylindrical apophysis is longer than the laminar apophysis; the row of spines and the basal spines are always well developed (Fig. 23). *Brachistoternus paulae* has three rows of ventral setae in the fifth metasomal segment, the usual disposition being 4-2-2 (Fig. 1), whereas in *B. alienus* the usual disposition is 4-2, although fewer than 10% of the specimens have an additional row of setae.

Description.—*Color:* General color light yellow with a dusky pattern. Prosoma with a dark stripe from the lateral eyes to the postocular furrow; anterior edge with black spots; ocular tubercle black; anterior and posterior longitudinal sulcus with an underlying dark stripe. *Pedipalps:* femur with a black spot at the articulation with the patella. Tergites I to IV with a light dark reticulation; V with two posterolateral dark spots. Metasomal segments I to III dorsally with two posterolateral dark spots; I to IV with a narrow stripe; segments I to IV ventrally with two lateroventral stripes; V with two lateroventral stripes and a median stripe that does not converge with the lateroventral stripes in the posterior margin of the segment. Some specimens are almost completely yellow, without the dusky pattern.

Morphology: Measurements of male holotype and a female paratype (MACN-Ar 10083) in Table 1. *Prosoma:* Chelicerae with two subdistal teeth; anterior edge with a slight median bulge and six setae, two on each side and two in the middle; tegument with coarse granules near the anterior margin, the rest finely granular; anterior and posterior longitudinal sulcus, lateral sulcus and postocular furrow deeply marked; ocular tubercle slightly anterior of the middle of the carapace with a slight interocular sulcus, eyes one diameter apart with a seta behind each eye. *Mesosoma:* tergites I to VI smooth near the anterior edge, the rest densely granular; VII smooth in the middle, the rest densely granular. *Metasoma:* segment I: ventral surface with scattered granulation and three pairs of ventral setae, lateral surface with scattered granulation, dorsally

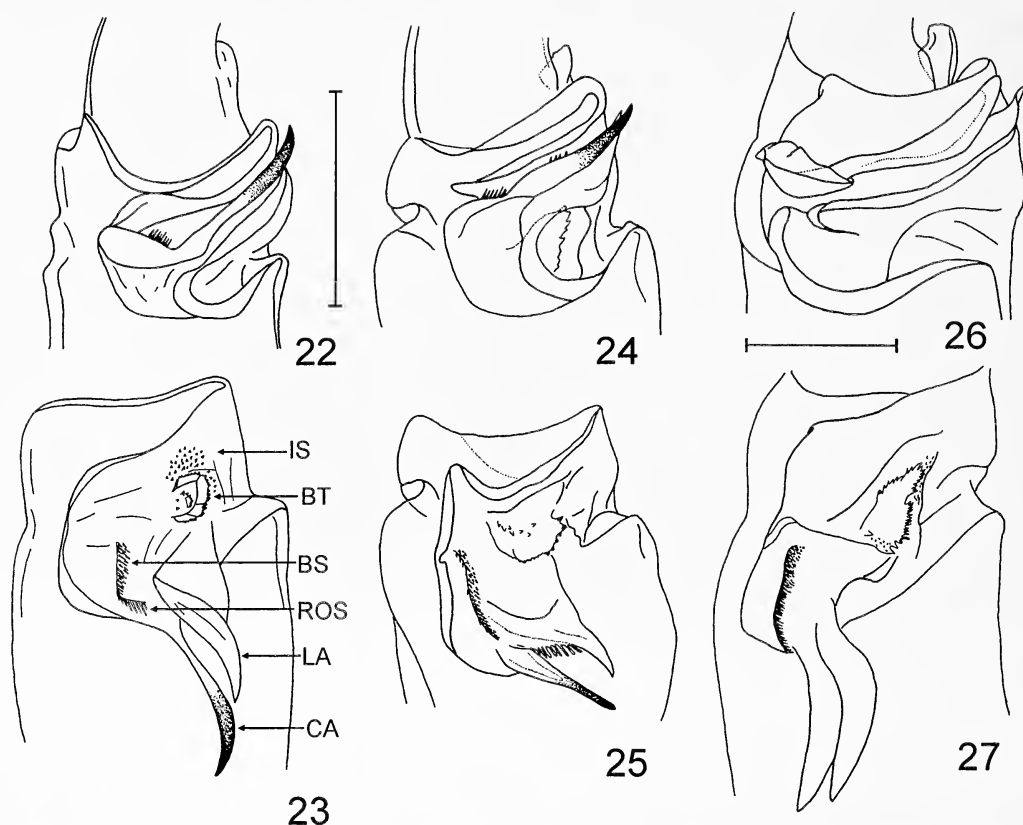
smooth, dorsosubmedian, dorsolateral and median lateral carinae extend the entire length of the segment and converge distally; segments II and III similar to segment I but less granular, with less well developed carinae and with four pairs of ventral setae; segment IV: dorsally smooth, lateral surfaces with sparse granulation, ventrally smooth with a large number of scattered setae; segment V ventral surface densely granular, ventromedian and ventrolateral carinae extend the entire length of the segment (Fig. 1); dorsal and ventral surfaces finely granular or smooth; ventral setae usually comprising 3 rows: 1 basal row of 3–5 setae, 1 median row of 1 or 2 setae, and 1 posterior row of 1 or 2 setae, in some specimens there is an additional row of 1 or 2 setae; in males the androvestigia (Cekalovic 1973) occupy almost 2/3 of the dorsal face (Fig. 2). Telson sparsely granular; vesicle with rounded ventral surface; aculeus slightly curved, of the same length as the vesicle (Fig. 10); kidney shaped gland of the dorsal surface (Roig Alsina & Maury 1981) absent.

Pedipalps: trichobothrial pattern, orthobothriotaxic type C: femur with 3 trichobothria: 1 d, 1 i and 1 e; patella with 3 v trichobothria and 13 trichobothria on its external face: 3 et, 1 est, 2 em, 2 esb and 5 eb; chela with 11 trichobothria on its prolateral face: 1 est, 2 et, 4 v, 1 esb and 3 eb; no intraespecific variation has been observed in this character (Fig. 21). Femur and patella without carinae, with scattered granulation on its anterior margin; chela stout with relatively short fingers (Figs. 6–9), smooth tegument, with a ventroexternal carina; in males the prolateral apophysis is well developed; movable finger with a central row of granules and 6 or 7 internal and external granules. *Legs:* finely granular; telotarsi I and II with the inner unguis 10 to 15 percent longer than the external. *Hemispermaphore* (Figs. 3–5): narrow distal lamina, shorter than the basal portion, with the external margin undulated; cylindrical apophysis poorly developed, shorter than the laminar apophysis; basal triangle well developed; row of spines generally absent, or if present, vestigial; internal spines and basal spines absent.

Variation.—Total length in males, 33–45 mm ($n = 30$; mean = 40.32), 34–45 mm in females ($n = 30$; mean = 42.15). Pectines with 19–27 pectinal teeth in females ($n = 30$;

Table 1.—*Brachistosternus paulae* n. sp.: measurements (mm), number of pectinal teeth and telotarsal setae of the male holotype (MACN-Ar 10082) and a female paratype (MACN-Ar 10083).

	Male holotype	Female paratype
Total length	42.50	41.00
Prosoma, length	4.00	4.50
Prosoma, anterior width	2.77	3.23
Prosoma, posterior width	4.24	4.85
Mesosoma, total length	18.00	17.30
Metasoma, total length	20.50	21.20
Metasomal segment I, length	2.50	2.83
Metasomal segment I, width	2.61	2.70
Metasomal segment I, height	2.00	2.18
Metasomal segment II, length	2.80	2.90
Metasomal segment II, width	2.30	2.30
Metasomal segment II, height	2.00	2.20
Metasomal segment III, length	3.00	2.90
Metasomal segment III, width	2.10	2.20
Metasomal segment III, height	2.00	2.00
Metasomal segment IV, length	3.90	3.70
Metasomal segment IV, width	2.00	2.10
Metasomal segment IV, height	1.80	1.80
Metasomal segment V, length	4.00	4.36
Metasomal segment V, width	2.00	2.02
Metasomal segment V, height	1.63	1.62
Telson, length	4.30	4.50
Vesicle, length	2.60	2.42
Vesicle, width	1.50	1.62
Vesicle, height	1.50	1.86
Aculeus, length	1.70	2.10
Pedipalp, total length	10.45	10.53
Femur, length	2.70	2.83
Femur, width	2.70	1.00
Patella, length	2.75	2.70
Patella, width	1.10	1.37
Chela, length	5.00	5.00
Chela, width	1.30	1.45
Chela, height	1.45	1.70
Movable finger, length	3.00	2.75
Number of pectinal teeth	27–27	24–24
Telotarsus I, ventrointernal setae	4	5
Telotarsus I, ventroexternal setae	4	4
Telotarsus I, dorsal setae	8	7
Telotarsus II, ventrointernal setae	6	5
Telotarsus II, ventroexternal setae	4	4
Telotarsus II, dorsal setae	11	10
Telotarsus III, ventrointernal setae	8	8
Telotarsus III, ventroexternal setae	8	9
Telotarsus III, dorsal setae	12	11
Telotarsus IV, ventrointernal setae	6	7
Telotarsus IV, ventroexternal setae	4	5
Telotarsus IV, dorsal setae	4	4



Figures 22–27.—Hemispermatophores of genus *Brachistosternus*; detail of the lobe region, top: closed aspect, bottom: open aspect. 22–23. *Brachistosternus* (*Leptosternus*) *alienus*, abbreviations: IS: internal spines; BT: basal triangle; BS: basal spines; ROS: row of spines; LA: laminar apophysis; CA: cylindrical apophysis. 24–25. *Brachistosternus* (*Ministernus*) *ferrugineus*; 26–27. *Brachistosternus* (*Brachistosternus*) *ehrenbergii*. Scale bars = 1 mm.

median = 23) and 22–29 in males ($n = 30$; median = 27). Length/height ratio of the pedipalp chela 3.05–3.41 in males ($n = 30$; mean = 3.29) and 2.90–3.25 in females ($n = 30$; mean = 3.14). Telotarsus I with 4 or 5 ventrointernal setae ($n = 40$; median = 5), 4 or 5 ventroexternal setae ($n = 40$; median = 5) and 7–9 dorsal setae ($n = 40$; median = 8). Telotarsus II with 5–7 ventrointernal setae ($n = 40$; median = 7), 4 or 5 ventroexternal setae ($n = 40$; median = 4) and 10–12 dorsal setae ($n = 40$; median = 12). Telotarsus III with 7–9 ventrointernal setae ($n = 40$; median = 8), 8 or 9 ventroexternal setae ($n = 40$; median = 8) and 10–13 dorsal setae ($n = 40$; median = 12). Telotarsus IV with 5–7 ventrointernal setae ($n = 40$; median = 7), 4–6 ventroexternal setae ($n = 40$; median = 4) and 4–6 dorsal setae ($n = 40$; median = 6). Fourth metasomal segment with 48–57 ventral setae ($n = 20$;

median = 53). Fifth metasomal segment with 8–13 ventrolateral setae ($n = 30$; median = 10), and 6–11 lateral setae ($n = 30$; median = 8).

Additional comments.—The hemispermatophore of *B. paulae* is the least developed of the genus. However a Chilean species (still unnamed) also presents such a scarce development of the internal structures, but a much longer distal lamina.

The number of pectinal teeth of *B. paulae* is similar in males and females, which is uncommon in genus *Brachistosternus* (Roig Alsina & Maury 1981; Ojanguren Affilastro 2000).

Although the morphology of *B. paulae* resembles the subgenus *Leptosternus*, its particular trichobothrial pattern does not allow for its inclusion in any of the known subgenera. The same situation occurs with *B. telteca*

(Ojanguren Affilastro 2000). The subgeneric division created by Maury (1973) is based on few characters and should be revised.

Distribution.—*Brachistosternus paulae* is endemic to Argentina in the north and center of Santa Cruz Province (Fig. 29). This area belongs to the “Patagonia” Phytogeographic Province, and to the “Monte” and “Patagonica” Scorpiological Areas.

HEMISPERMATOPHORES OF GENUS
BRACHISTOSTERNUS

Only the internal structures are compared, because the distal lamina and the basal portion are similar in the rest of the family.

The hemispermaphore of the subgenus *Leptosternus* Maury 1973 (Figs. 12, 15, 16, 22 & 23) has a basal triangle formed by two or more sclerified crests, that may be more or less developed depending on the species; the internal spines are beside the basal triangle, and they are always absent in *B. intermedius*, *B. zambrunoi* and *B. montanus*; and in some specimens of *B. alienus* (Ojanguren Affilastro 2001); the cylindrical apophysis is tubular shaped; the row of spines is a continuation of the basal spines, forming the same structure.

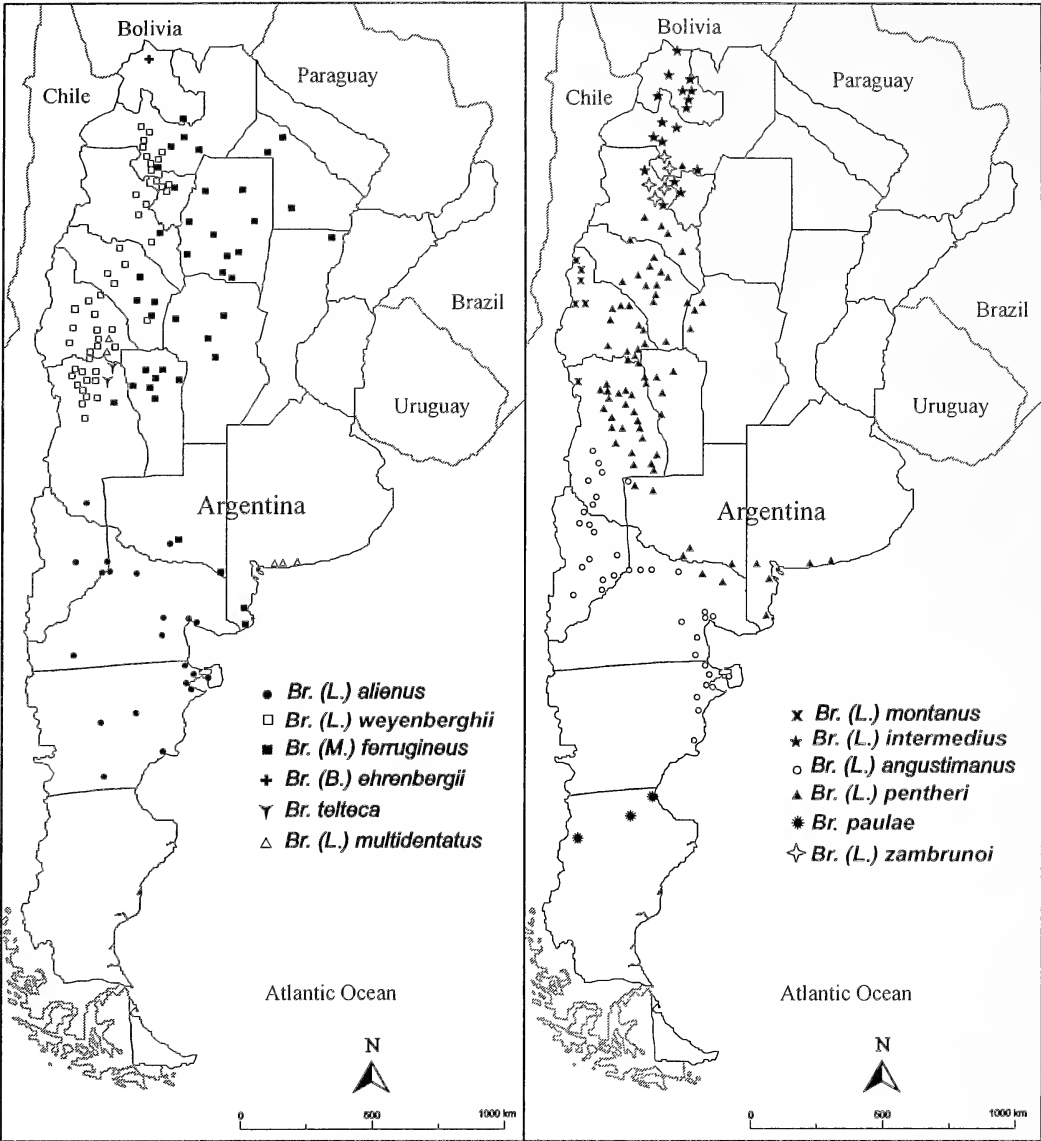
The hemispermaphore of the subgenus *Brachistosternus* Pocock 1893 (Figs. 26 & 27) is similar to that of subgenus *Leptosternus* but its cylindrical apophysis is dorsoventrally flattened and is quite similar to the laminar apophysis; the basal triangle is well developed and has an elongated characteristic shape; the internal spines are reduced to small granules; the row of spines is a continuation of the basal spines as in subgenus *Leptosternus*.

The hemispermaphore of the subgenus *Ministernus* Francke 1985 (Figs. 24 & 25) has some peculiarities, the internal spines are absent; the row of spines is separated from the basal spines by the cylindrical apophysis. The basal triangle is similar to that of subgenus *Leptosternus* in *B. (Ministernus) ferrugineus*, but in *B. (Ministernus) andinus* Chamberlin 1916 from Peru, the basal triangle is a small tubercle covered by small spines (Maury 1978b).

Brachistosternus telteca and *B. paulae* have hemispermaphores similar to that of subgenus *Leptosternus*. *Brachistosternus telteca* lacks the internal spines and its basal triangle is poorly developed (Ojanguren Affilastro 2000).

KEY TO THE ARGENTINIAN SPECIES OF *BRACHISTOSTERNUS*

- 1. Pedipalp chela with 9–12 v trichobothria and 5 eb, patella with 3 v trichobothria and 1 esb (Fig. 17) *Brachistosternus (Ministernus) ferrugineus* (Thorell 1876)
- Pedipalp chela with 4–6 v trichobothria and 3 eb, patella with 3–7 v trichobothria and 2 esb 2
- 2. Pedipalp chela with 6 v trichobothria; patella with 4 v trichobothria (Fig. 20)
..... *Brachistosternus telteca* Ojanguren Affilastro 2000
- Pedipalp chela with 4 or 5 v trichobothria; patella with 3 or 5–7 v trichobothria 3
- 3. Pedipalp patella with 5–7 v trichobothria (Fig. 19)
..... *Brachistosternus (Brachistosternus) ehrenbergii* (Gervais 1841)
- Pedipalp patella with 3 v trichobothria 4
- 4. Pedipalp chela with 4 v trichobothria (Fig. 21) *Brachistosternus paulae* new species
- Pedipalp chela with 5 v trichobothria (Fig. 18) *Brachistosternus (Leptosternus)* 5
- 5. Telson with 4 better developed granules on the ventral face of the vesicle, 2 near the aculeus and 2 in the median part (Fig. 11)
..... *Brachistosternus (Leptosternus) weyenberghii* (Thorell 1876)
- Telson without 4 better developed granules on the ventral face of the vesicle (Fig. 10) 6
- 6. Distal projection of telotarsus IV highly developed (Fig. 14)
..... *Brachistosternus (Leptosternus) multidentatus* Maury 1984
- Distal projection of telotarsus IV not highly developed (Fig. 13) 7
- 7. Basal triangle of the hemispermaphore well developed, internal spines usually present (Fig. 23) 8
- Basal triangle of the hemispermaphore poorly developed, internal spines always absent (Fig. 12) 9
- 8. Scorpions from small to medium size, males from 34–43 mm, females from 36–41 mm,



28

29

Figures 28 & 29.—Maps with the distribution of the Argentinian species of the genus *Brachistosternus*.

- internal spines usually present but in some cases, absent *Brachistosternus (Leptosternus) alienus* Lönnberg 1898
- Scorpions from medium to large, males from 46–85 mm, females from 60–91 mm; internal spines always present 10
- 9. Distal lamina straight and longer than the basal portion of the hemispermatophore (Fig. 15) *Brachistosternus (Leptosternus) zambrunoi* Ojanguren Affilastro 2002
- Distal lamina curved and shorter than the basal portion of the hemispermatophore (Fig. 16) 11
- 10. Pedipalp chela length/height ratio from 2.91–3.43 in males, and from 2.80–3.20 in females; ventral setae of the fifth metasomal segment usually comprising 2 rows of 2 setae each *Brachistosternus (Leptosternus) pantheri* Mello Leitão 1931

- Pedipalp chela length/height ratio from 3.47–4.14 in males, and from 3.40–3.63 in females; ventral setae of the fifth metasomal segment comprising 2–5 rows, the first one of 4 setae and the rest of 2 setae each
 *Brachistosternus (Leptosternus) angustimanus* Ojanguren Affilastro & Roig Alsina 2001
11. Pedipalp chela length/height ratio from 2.60–3.00 in males and from 2.62–2.90 in females; ventral setae of the fifth metasomal segment usually comprising 3 rows
 *Brachistosternus (Leptosternus) intermedius* Lönnberg 1902
- Pedipalp chela length/height ratio from 3.14–3.48 in males and from 3.06–3.23 in females; ventral setae of the fifth metasomal segment usually comprising 4 or more rows
 *Brachistosternus (Leptosternus) montanus* Roig Alsina 1977

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LIFE CYCLE, REPRODUCTIVE PATTERNS AND THEIR YEAR-TO-YEAR VARIATION IN A FIELD POPULATION OF THE WOLF SPIDER *PIRATA PIRATICUS* (ARANEAE, LYCOSIDAE)

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ABSTRACT. Patterns of growth, phenology and reproduction were studied in a field population of the wolf spider *Pirata piraticus* from November 1997 until October 1998 and in June 1999 to unravel the intrapopulation variation and co-variation of these traits. Individuals of *P. piraticus* overwinter as juveniles of different instars while adults were found from the end of April until September. Strong year to year variation in the age and size of overwintering juveniles was present, resulting in a corresponding difference in adult size in the subsequent breeding season. The main period of reproduction occurred from May until August with larger individuals breeding earlier in the season. The size at which adults breed was also significantly different in the successive years. Clutch mass (cocoon mass), clutch volume and fecundity are dependent on the size of the female according to a weakly negative allometric relationship. The differences in those reproductive traits between the successive years are therefore proportionate to the differences in female size. This was in clear contrast to egg size, a life history trait that shows much less variation and appears to be independent of female size. Therefore, egg size was not significantly different between spring 1998 and spring 1999. There is, however, some variation in fecundity due to egg size and number independent of female size. When corrected for female size, females with larger eggs produce relatively fewer eggs indicating a trade-off between these two reproductive characters.

Keywords: Life history, reproduction, egg size, fecundity, year-to-year variation, *Pirata piraticus*

In wolf spider populations, considerable variation can be observed in phenology (life cycle timing), growth rate, adult size and reproductive output (e.g. Petersen 1950; Edgar 1972; Kessler 1973; Humphreys 1976; Toft 1979; Alderweireldt & Maelfait 1988; Simpson 1993; Maelfait & Hendrickx 1998; Samu et al 1998; Buddle 2000). Most of these studies dealt with only one life history trait and did not look for interrelations between these traits. However, the variation and co-variation of these traits is of particular importance to understand the costs and benefits of a specific life history trait (Stearns 1992; Roff 1992) and can be used to predict changes in life history patterns when environmental conditions change.

In this study we analyzed the life-history of a field population of a common wolf spider *Pirata piraticus* (Clerck 1757) in Belgium.

The life-cycle of a field population of this lycosid in Denmark has already been analysed by Toft (1979), who demonstrated that adults of this species appear in spring and females produce one or (possibly) two egg sacs in summer. The hatched juveniles grow during summer and autumn and overwinter as sexually differentiated juveniles or subadults. Juveniles that are born at the end of the summer overwinter a first time as juveniles (not yet sexually differentiated) and a second time during the subsequent winter before they reach the adult stage in May. Laboratory experiments conducted by Schaeffer (1976a, b) revealed that temperature as well as photoperiod are important factors that determine growth and development of this species. Data about intrapopulation size differences, year-to-year variation, and the variation and covariation of

adult and reproductive traits are, however, lacking. This information might be of importance to understanding the evolution of the life-history pattern of this species and the interpopulation variation therein.

METHODS

Collection of the animals.—All animals were captured from the same locality, a tidal marsh (Galgenschoor) situated north of the city of Antwerp (Flanders, Belgium) along the tidal river Schelde (51°18' N, 4°18' E). The vegetation consisted mainly of common reed (*Phragmites australis*). Within this tidal marsh, the same area of approximately 10 by 10 m was used as the sampling site. All animals were captured by hand picking. Pitfall traps are useless in these tidal marshes because of the frequent inundations and because pitfall captures have a serious bias caused by differences in activity between the different developmental stages and sexes (Maelfait & Baert 1975; Maelfait 1996). After measuring life history traits of all captured specimens, they were deposited at the Department Biology at Ghent University (Belgium). Sampling was carried out every one or two months from November 1997–October 1998 resulting in a total of 9 sampling occasions, more or less evenly distributed throughout the year. Sampling took place in 1997 on 19 November and in 1998 on 26 February, 1 April, 29 April, 15 May, 17 June, 10 August, 18 September and 21 October. An additional sample was taken 3 June 1999.

Growth and phenology.—For analysis of phenology and growth patterns in the field, only the specimens captured in 1997 and 1998 were used. All animals were kept individually in plastic tubes to avoid cannibalism and the exchange of egg sacs between females. Once transferred to the laboratory, animals were kept in a freezer at -10°C before measurements were made. All animals were sorted by developmental stage and in the case of adult and larger juvenile spiders also by sex. The criteria to determine a juvenile as a sexually differentiated male was the presence of (slight) swollen palps, while the presence of two (sometimes very small) reddish dots in the central part of the epigastric fold was used to assign an individual as a sexually differentiated female. To determine the size of the animals, the carapace width was measured at

its widest point (Hagstrum 1971; Alderweireldt & Maelfait 1988), to the nearest 0.03 mm using a graticule eyepiece fitted to a Wild stereomicroscope.

Reproductive traits.—Patterns of reproduction were analysed on females originating from the sampling campaign conducted on 17 June 1998 and on females from a second sample, conducted on 3 June 1999 during which only females with an egg sac were collected to study year to year variation in reproductive characteristics. The number of eggs or young present in the egg sac was taken as a measure of fecundity. To obtain a measure of clutch mass, the egg sac (including eggs and/or juveniles) was weighted to the nearest 0.1 mg on an Ohaus Galaxy 110 electronic balance. The weight of the cocoon itself was negligible compared to its content ($< 0.1\%$).

Before measuring the size of the eggs, they were stored for approximately one month in ethanol 70%. After this treatment, the egg shell becomes fully expanded and size differences between developing and undifferentiated eggs can be neglected. As the shape of the eggs is ellipsoid, egg length as well as egg width was measured to the nearest 0.01 mm. Egg volume was calculated according to the formula: egg volume = $\Pi/6 \times (\text{egg length}) \times (\text{egg width})^2$.

The product of egg volume and egg number was calculated to obtain a measure of clutch volume. Female mass and, if an egg sac was present, clutch mass, of females captured on 3 June 1999 were additionally weighed to the nearest 0.1 mg on an Ohaus® Galaxy 110 electronic balance.

To correlate reproductive traits with the size of the mother, carapace width was cubed to make it proportional to volumetric measurements like fecundity, clutch volume, clutch mass and egg size.

Data analysis.—Differences in proportions of adult versus juvenile spiders over the different sampling dates were analysed by an $R \times C$ independence test (Sokal & Rohlf 1995). To test for size differences between the developmental stages and the different sampling dates, ANOVA was used if assumptions for normality and homogeneity of variance were met. Otherwise, we resorted to non-parametric (Kruskal-Wallis) ANOVA. Multiple comparisons of the different groups were performed with Scheffé test.

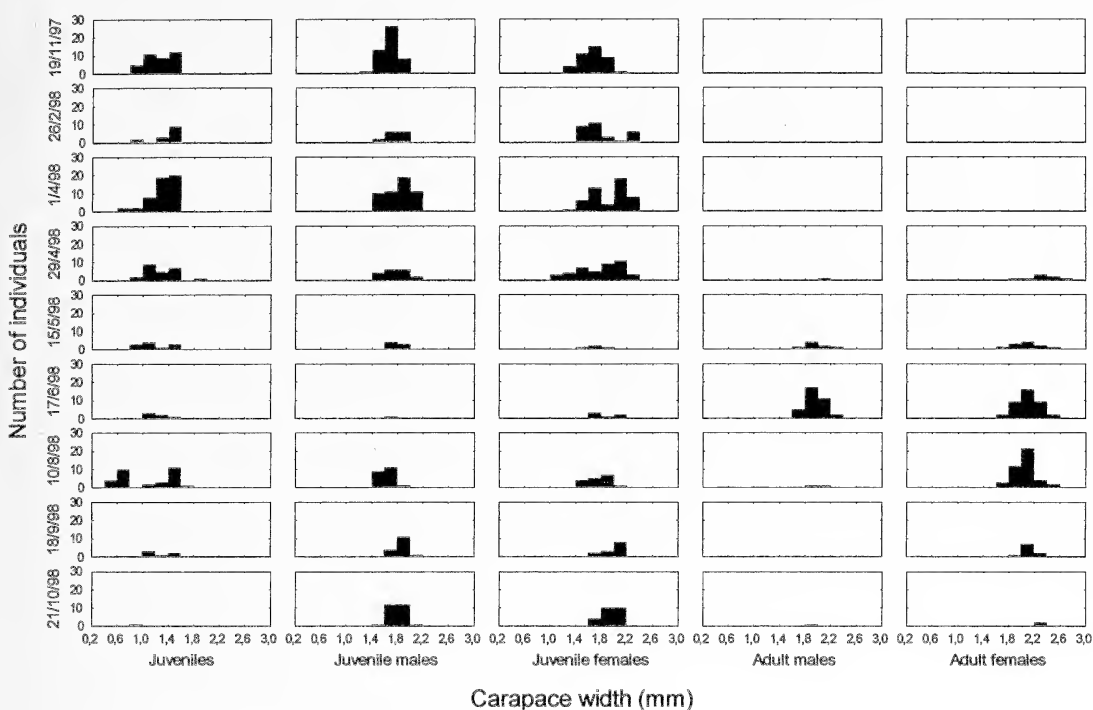


Figure 1.—Frequency distributions of the different developmental stages according to carapace width (mm).

The size distribution of a particular group was analysed by mixture analysis, in which model selection was based on the likelihood ratio test (LR-test). The test was performed by the Mixture 1 program, developed to analyse patterns of fluctuating asymmetry (Van Dongen et al. 1999).

RESULTS

Phenology.—The numbers and the proportions of the different developmental stages over the different samples are depicted graphically on Fig. 1. From November 1997 until the beginning of April 1998, only juvenile spiders were found. From the end of April onwards, adult spiders appear while juvenile spiders were still present. Sexually differentiated males and females were recorded in almost equal numbers over the different sampling dates. The highest proportions of sexually differentiated juveniles were recorded in spring and autumn, while they were almost totally absent in May and June 1998. From November to mid-June, the number of small, sexually undifferentiated spiders present in the samples showed a somewhat similar pattern compared to the number of sexually differentiated ju-

veniles. A high peak in the number of juveniles was observed in August 1998 when juveniles emerged from the egg sac of the adult females. After that a different growth pattern in comparison with the previous year is observed, as small juveniles are already totally absent in October 1998. This difference in proportion of juveniles on October 1998 compared to November 1997 is significant ($\chi^2 = 19.80$; $P < 0.0001$).

Adult spiders emerge from overwintering sexually differentiated and undifferentiated juvenile spiders, as the proportion undifferentiated juveniles encountered during winter differed significantly from the proportion non-adult spiders in May 1998 (29.6% versus 15.2%; $\chi^2 = 0.15$; $P = 0.015$).

The highest proportion of males (40.7%) was recorded on June 1998 and almost all died by August 1998. Females were present until October 1998 with the highest proportions recorded on June 1998 (44.2%) and August 1998 (37.2%).

Growth.—The distribution of the carapace width of the spiders of the different developmental stages on the different sampling dates

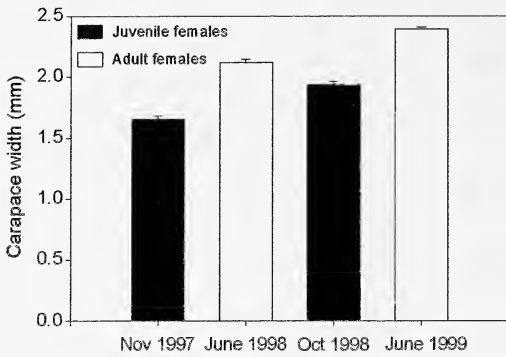


Figure 2.—Carapace width (mm) of juvenile females in their hibernating stage and their adult size in the subsequent spring.

are presented on Fig. 1. A significant bimodality in size distribution is observed in juveniles captured in August 1998 ($LR = 58.77$; d.f. = 3; $P < 0.0001$). Juvenile females are on average significantly larger than juvenile males and significantly different over the different sampling dates (two-way ANOVA; sex-effect: $F_{1, 410} = 5.07$; $P = 0.025$; date effect: $F_{8, 410} = 10.3$; $P < 0.0001$; interaction: $F_{8, 410}$; $P = 0.39$). Sexually differentiated juveniles captured in November 1997 are significantly smaller than those captured in April, September and October 1998 ($P < 0.0002$). This implies that sexually differentiated juveniles still increase in size before they reach the adult size.

A comparison of differences in carapace width between males and females could only be performed on adults captured in May, June and August, when a sufficient number of individuals of both sexes were present in the samples. Males have a significantly smaller carapace width than females (ANOVA; $F_{1, 134}$; $P < 0.0002$). Female size shows a significant heterogeneity over the different sampling dates (ANOVA; $F_{5, 105}$; $P = 0.003$), with females captured at the end of April being significantly larger than females captured in June and August ($P < 0.05$). Although not significant, the same pattern also appears to exist for males (ANOVA; $F_{2, 42}$; $P = 0.14$).

The larger overwintering juvenile females in October 1998 compared to November 1997 seems to result in a corresponding increase in size of adult females captured on June 1999 compared to the size of the adult females captured in June 1998 (Fig. 2) (ANOVA; year-

effect $F_{1, 128} = 96.8$; $P < 0.0001$; year x stage affect; $F_{1, 128} = 0.03$; $P = 0.87$).

Reproduction.—Females with an egg sac were found in May 1998 (60.5%), August 1998 (71.4%) and September 1998 (20.0%). In May 1998, all females had eggs in their egg sac while in August 1998, 18 out of 30 females with an egg sac had first instar juveniles in their egg sac. Female size is not significantly different between females with and females without an egg sac ($F_{1, 73}$; $P = 0.43$).

As mentioned above, the analysis of the variation and the relationship of reproductive traits and adult female size was conducted on individuals captured in June 1999. There is a great variability for female size measured as carapace width³ (C.V. = 12.5%); fecundity (C.V. = 17.2%) and clutch volume (C.V. = 17.1%). This is in clear contrast with the variation in egg volume (C.V. = 3.1%), which is very consistent within the population.

The results of the correlation between female size and female mass with the different reproductive traits are presented in Table 1. Clutch mass, clutch volume and fecundity are in all cases positively correlated with carapace width³. When female mass is taken as a measurement of female size, only clutch mass in the untransformed data, and clutch mass and fecundity in the log transformed data are significantly correlated. No significant relationship is observed between the two measurements of female size and egg size. Higher correlation coefficients are observed between carapace width³ and the reproductive traits than for female mass and the reproductive traits. A better fit of the data is also observed when both variables are log transformed (higher r -values for all reproductive trait variables). All reproductive traits show negative allometry with female size (slope < 1). However, this is only significant for female mass compared to carapace width³, indicating that larger females have a relatively lower weight compared to smaller females.

A significant negative correlation between egg size and the residual values of log fecundity on log carapace width³ ($r = -0.38$; $P = 0.045$) reveals that a trade-off between egg size and fecundity is present (Fig. 3). This negative relationship is not due to the fact that females with larger eggs have a lower clutch volume as shown by the lack of a relationship between egg size and the residual values of

Table 1.—Regression equations between the untransformed and log transformed measurements of female size and some reproductive traits (n = number of individuals). (*) in the log transformed data indicate significant negative allometry (slope < 1; $P < 0.05$).

	n	r	P	Intercept	Slope
Carapace width ³					
Female mass	28	0.70	<0.0001	7.84	1.36
Cocoon mass	28	0.53	0.004	5.19	0.92
Number of offspring	28	0.40	0.034	18.79	2.51
Egg size	28	0.02	0.937	0.36	0.00
Reproductive output	28	0.45	0.016	5.86	0.96
Female mass					
Cocoon mass	28	0.47	0.011	6.62	0.42
Number of offspring	28	0.33	0.089	25.40	1.05
Egg size	28	−0.10	0.622	0.38	0.00
Reproductive output	28	0.32	0.098	9.77	0.35
Log carapace width ³					
Log female mass	28	0.72	<0.0001	0.61	0.72*
Log cocoon mass	28	0.59	0.001	0.30	0.83
Log number of offspring	28	0.45	0.017	0.80	0.81
Log egg size	28	0.00	0.986	1.14	0.01
Log reproductive output	28	0.48	0.010	0.35	0.81
Log female mass					
Log cocoon mass	28	0.52	0.004	0.17	0.75
Log number of offspring	28	0.38	0.044	0.73	0.70
Log egg size	28	−0.09	0.641	−0.36	−0.06
Log reproductive output	28	0.37	0.051	0.36	0.64

log clutch mass on log carapace width³ ($r = -0.09$; $P = 0.65$; Fig. 4).

When corrected for female size, no differences between the successive years are noted for fecundity (ANCOVA; $F_{1,49} = 0.39$; $P = 0.54$; Fig. 5) and clutch volume (ANCOVA; $F_{1,47} = 0.64$; $P = 0.2$; Fig. 6). Slopes of both regressions are not significantly different ($P >$

0.56) . Egg size is also remarkably similar in 1998 and 1999 (ANOVA; $F_{1,48} = 0.27$; $P = 0.6$; Fig. 7).

DISCUSSION

The observed life cycle of *Pirata piraticus* for 1998 is in agreement with the patterns observed by Toft (1979). From November 1997

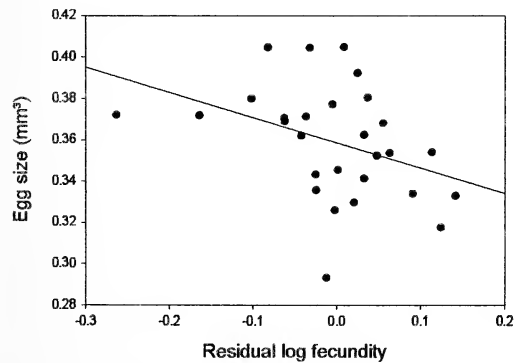


Figure 3.—The relationship between egg size and the residuals of the regression of log fecundity on log female carapace width³.

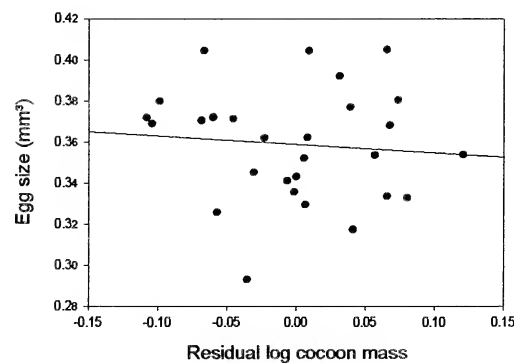


Figure 4.—The relationship between egg size and the residuals of the regression of log clutch mass on log female carapace width³.

until end of April 1998, only juveniles spiders were found. The main period of growth occurs from the second half of June, the period in which the spiderlings emerge until the beginning of the winter period (second half of September). In August, a clear bimodality is observed in the size of the juveniles. This size distribution implies the presence of two different cohorts or time periods at which juvenile spiders are released. As suggested by Toft (1979), it is likely that the group of smaller juveniles originates from a second egg sac produced by the females. The production of a second sac has also been observed frequently in the laboratory (F. Hendrickx, pers. obs.).

Adults that appear early in the breeding season (May) are larger compared to those found in the central period of the breeding season (June–August). As suggested by Alderweireldt & Maelfait (1989), it is likely that these larger individuals overwintered twice before reaching the adult stage.

Perhaps the most striking result is the pronounced difference in size and proportion of juveniles between the successive winters, which demonstrates that growth rate might show strong year-to-year variation. Although to a lesser extent, this year-to-year variation was also observed by Den Hollander (1971) in which ten populations of the *Pardosa pullata* (Clerck 1757) group were studied. Good growth conditions in autumn, possibly due to high temperature or food availability (Schmoller 1970; De Keer & Maelfait 1987; Beck & Connor 1992) might be responsible for the observed differences. It is also important to note that density dependent cannibalism is observed in wolf spiders (Wagner & Wise 1996; Samu et al. 1999) in which larger individuals of the population prey on smaller individuals. Such cannibalism could also be the cause of the absence of small juveniles and the dominance of larger juveniles in autumn of 1998. The larger size of the juveniles in autumn 1998 compared to autumn 1997 is also reflected in the larger adult size in the subsequent spring. This implies that growth conditions in the previous year are largely responsible for the ultimate size of the adults. Beck & Connor (1992) obtained similar results for the crab spiders *Misumenoides formosipes* (Walckenaer 1837). Their study revealed that 90% of the variation in adult size was explained by the variation in final weight of the subadult stage. As all the

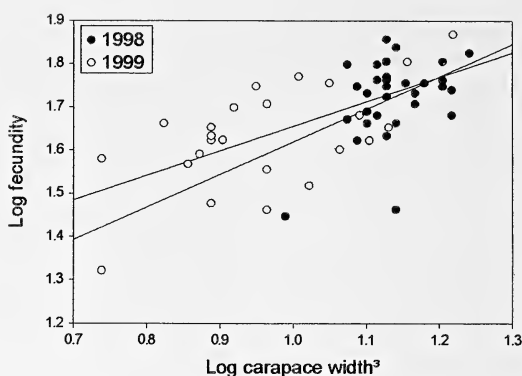


Figure 5.—The relationship between log female carapace width³ and log fecundity in June 1998 and June 1999.

individuals captured in autumn 1998 in our study were already sexually differentiated, it is likely that all these individuals completed their life cycle in about one year. This means that the adult spiders captured in 1999 were larger than the spiders captured in 1998, although their period of growth was shorter.

Concerning the reported interspecific and interpopulation differences in ratio of one-versus two-year old individuals (Schmoller 1969; Den Hollander 1971; Edgar 1972), it is of crucial importance to compare data over several breeding seasons. Edgar (1972) for example recorded interpopulation differences in the proportion of one and two year old individuals in two populations of *Pardosa lugubris* (Walckenaer, 1802). As both populations were sampled in different years, these results have to be interpreted with caution. Additionally, it is not clear whether the two populations contain the same species, as *P. lugubris* comprises a complex of related species (Töpfer-Hoffmann et al. 2000) that have distinct distribution patterns and habitat choices (Hendrickx et al. 2001).

Size of the adult females showed considerable variation within a breeding season with larger individuals breeding earlier in the season. According to the results obtained by Toft (1979) for *P. piraticus* and Alderweireldt & Maelfait (1988) for *Pardosa amentata* (Clerck 1757), it is likely that those larger individuals are descendants of the second egg sac of females that reproduced during summer 1996. The high variability in clutch mass and fecundity is positively correlated with the size of the female. Studies conducted by Kessler

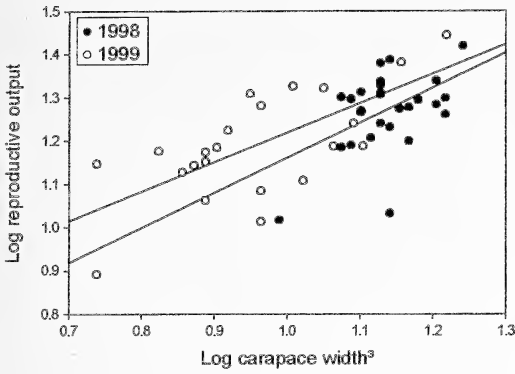


Figure 6.—The relationship between log female carapace width³ and log reproductive output in June 1998 and June 1999.

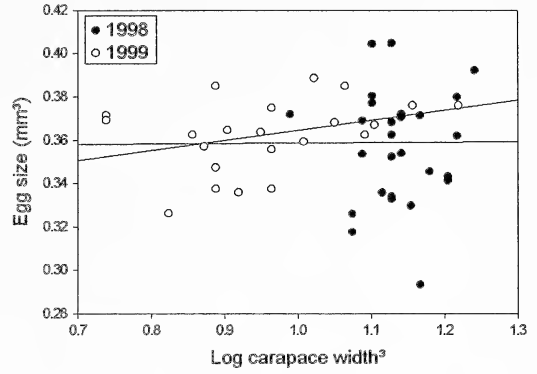


Figure 7.—The relationship between log female carapace width³ and egg size in June 1998 and June 1999.

(1973), Fritz & Morse (1985) and Kreiter & Wise (2001) revealed that foraging success might be responsible for the additional variation in reproductive success. As egg size is independent of female size, the observed increase in clutch volume and clutch mass with maternal size is due to an increased fecundity rather than due to an increase in egg size. This is in agreement with the results of other studies conducted on intrapopulation variation in reproductive traits in spiders (Fritz & Morse 1985; Simpson 1993).

When the effect of female size on fecundity was ruled out, a significant negative correlation between fecundity and egg size was observed. Therefore, this additional variation in fecundity due to egg size variation confirms a trade-off between egg size and fecundity (Stearns 1992). Because maternal fitness is the product of offspring number and offspring fitness, maternal fitness is determined by the curve relating offspring fitness to offspring size (Smith & Fretwell 1974; Parker & Begon 1986; Lloyd 1987), which implies that the optimal offspring size a female produces in a particular environment is at the offspring size where an increase in size does not compensate for the related decrease in fecundity and vice versa. The observed lack of correlation between egg size and female size might therefore be expected if offspring fitness is independent of maternal size, as has been observed in a large number of other invertebrates (reviewed in Fox & Czeback 2000).

We found that carapace width³ is a better predictor for size related reproductive char-

acteristics like fecundity and clutch volume. This is probably due to the fact that carapace width³ is a better estimate of female size than female mass is. Carapace width is independent of female condition after egg sac production and therefore a more reliable indicator for female size compared to female mass. Indeed, after the production of the egg sac, females can increase in weight due to feeding; leading to an underestimation of the relative amount of resources devoted to reproduction. Our results also demonstrate that almost all reproductive traits tended to show negative allometry with measurements of reproductive traits. It is important to take this allometry into consideration if a comparison in reproductive traits is made between samples of a different female size (Reist 1986; Roff 1992).

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**DESCRIPTION OF THE FEMALES OF *ANAPIS*
CASTILLA AND *ANAPISONA BORDEAUX*
(ARANEAE, ANAPIDAE)**

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ABSTRACT. The females of *Anapis castilla* Platnick & Shadab from the state of Amazonas and *Anapisona bordeaux* Platnick & Shadab from the state of Rio Grande do Sul both in Brazil, are described.

Keywords: Neotropical region, taxonomy, morphology

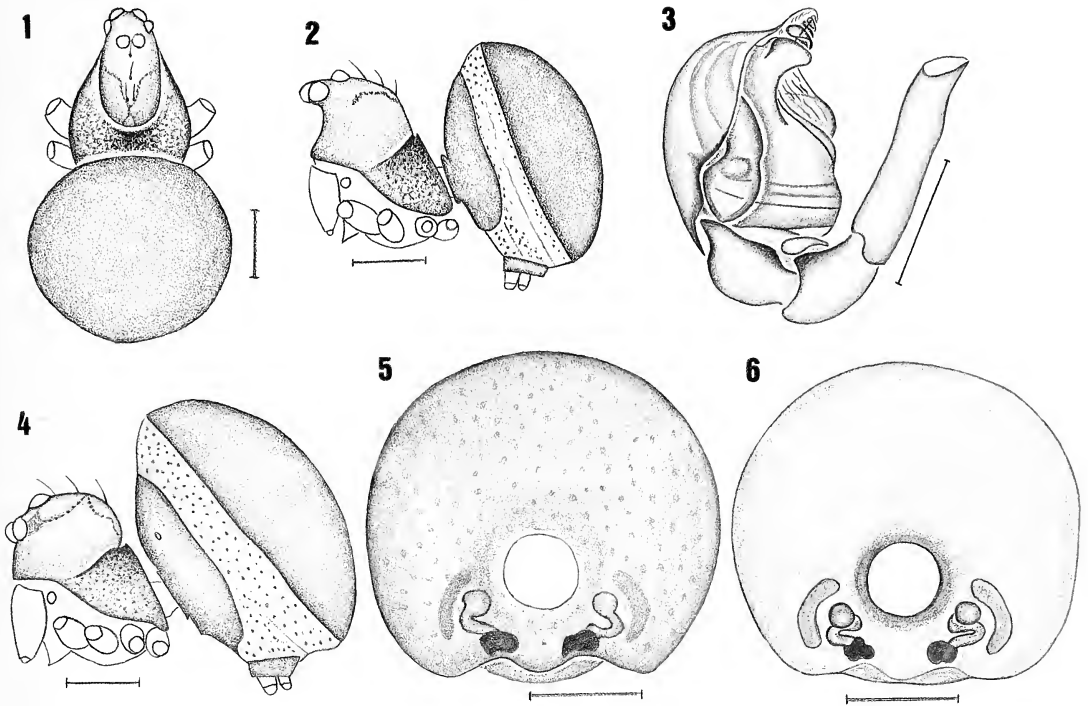
The Neotropical genera *Anapis* Simon and *Anapisona* Gertsch were revised by Platnick and Shadab (1978, 1979). The genus *Anapis* currently includes 22 species, of which 11 are known from both males and females, nine only from females and two only from males. Two species have been recorded from Brazil: *A. hetschki* (Keyserling 1886) from Santa Catarina and *A. discoidalis* (Balogh & Loksa 1968) from Pará (Platnick 2002). The genus *Anapisona* includes 13 species, seven known from couples, two only from females and four only from males. Two species have been recorded from Brazil: *A. schuhi* Platnick & Shadab 1979, from Amazonas, and *A. platnicki* Brignoli 1981, from Santa Catarina (Platnick 2002).

We studied several specimens of Anapidae collected in the Brazilian region and verified that they belong to species previously known only from the male holotypes: *Anapis castilla* Platnick & Shadab 1978 and *Anapisona bordeaux* Platnick & Shadab 1979. Apparently both species are relatively rare ground dwellers inhabiting the litter layer. They are here recorded for the first time from Brazil.

A very unusual distribution was presented by *A. bordeaux*. The new locality record for this species (Atlantic Forest remnant in the northeast highlands of Rio Grande do Sul, Brazil) is located approximately 5000 km from the type locality (Bordeaux Mountains in the U.S. Virgin Islands). Two hypotheses must be considered: introduction or a wide

range distribution. However, the introduction hypothesis is improbable since the locality where these specimens were collected, in southern Brazil, is not very influenced by human activities. The Centro de Estudos e Conservação da Natureza Pró-Mata area comprise mountain out slopes from 500 to approximately 950 m elevation. It is characterized by Mixed Ombrophilous Forest, with Dense Ombrophilous forests and Savannahs, and by humid to very humid climate, with temperatures below 15 °C during the winter season (Bertoletti & Teixeira 1995). Unfortunately, detailed environmental data about the type locality of the holotype is not available for comparison. This is probably a case of wide range distribution considering that the Neotropical spider fauna is poorly known. At least two similar cases are cited in the literature. The holotype for the anyphaenid species *Otoniella quadrivittata* (Simon) was described from Venezuela and later recorded in northern Argentina (Brescovit 1996:61–62). The zodariid *Leprolochus birabeni* Mello-Leitão is distributed from northeastern Brazil, with a great number of records in Paraguay and Argentina (Jocqué 1988, fig. 1).

All measurements are in millimeters. The studied specimens are deposited in the collections of the Instituto Butantan (IBSP), Instituto Nacional de Pesquisas da Amazônia (INPA, C. Magalhães); Museu de Ciências e Tecnologia da PUC/RS (MCTP, A.A. Lise); Museu de Ciências Naturais da FZB/RS



Figures 1–6.—*Anapis castilla* Platnick & Shadab, male, body: 1. dorsal view; 2. lateral view; palp: 3. retrolateral view; female, body: 4. lateral view; epigynum: 5. ventral view; 6. dorsal view. Scale = 0.25 mm.

(MCN, E.H. Buckup) and Staatliches Museum für Naturkunde Karlsruhe (SMNK, H. Höfer).

Anapis castilla Platnick & Shadab

Figs. 1–6

Anapis castilla Platnick & Shadab 1978:22, fig. 20 (male holotype from Berlese sample of forest litter collected at the edge of the Amazon River at Ramón Castilla (5 km NW. of Leticia, Colombia), Loreto, Peru, 23 February 1972, S. & J. Peck, deposited in Field Museum of Natural History, Chicago, not examined).

Material examined.—BRAZIL: *Amazonas*: 27 males, 31 females, Manaus, Rio Solimões, Canal Janauari (03°20'S, 60°17'W, "água mista"), 1988, J. Adis et al. (MCN 23687; IBSP 34436–34440; SMNK; INPA); 7 ♂, 2 ♀, with same locality data, 1 March 1988 (MCN 23686).

Diagnosis.—Females of *A. castilla* are distinguished from other *Anapis* females by strong sclerotizations around the opening of the copulatory ducts (Figs. 5–6).

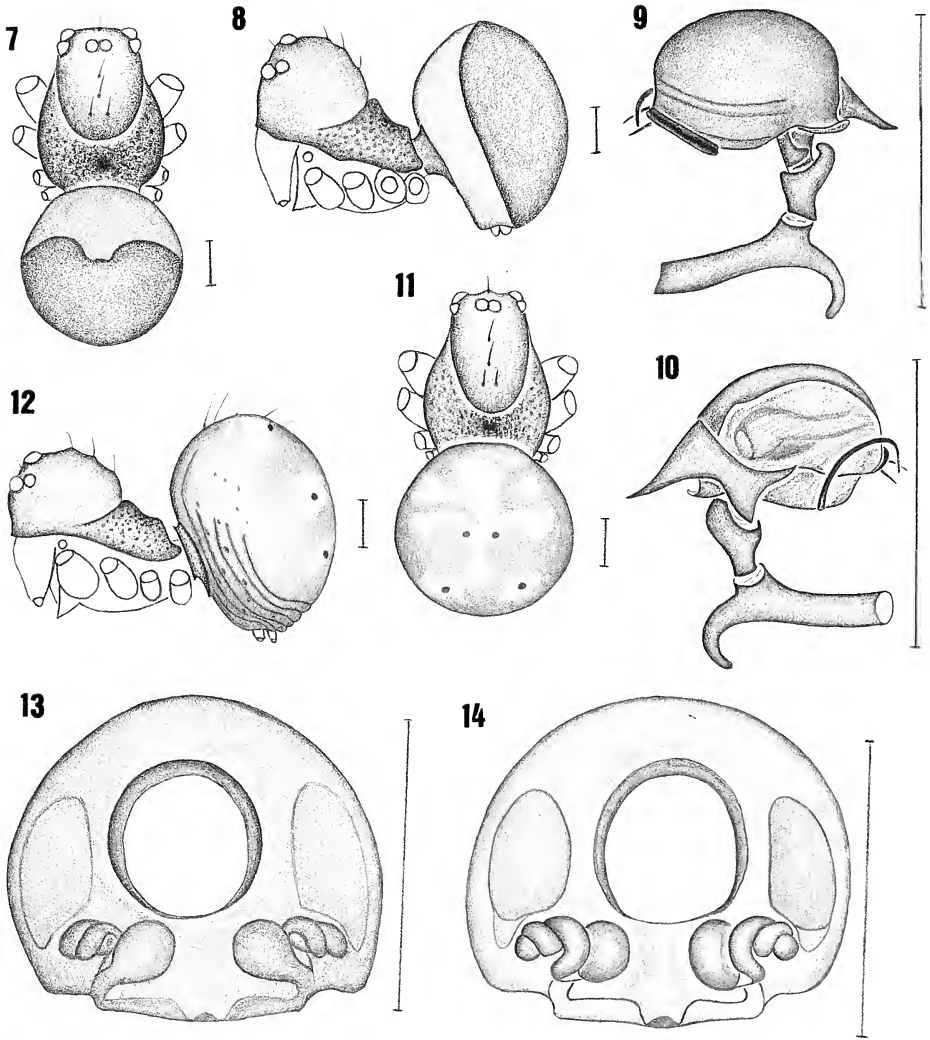
Description.—*Male*: Described by Platnick & Shadab (1978). Body and palp are here presented in Figs. 1–3.

Female: Carapace, sternum and abdominal scutum brownish orange. Legs orange. Tibia I with one very short distal prolateral cusp. Anterior portion of carapace not projecting, as in male (Fig 4). Anterior lateral eyes separated by about one third of their diameter. Scutum of abdomen smooth, covering the dorsum entirely, with very small and abundant lateral punctuations (Fig 4). Surface of ventral scutum covered with irregularly dispersed and very slightly sclerotized depressions. Measurements. Total length 1.27. Carapace 0.62 long, 0.50 wide, 0.40 high. Abdomen 1.18 long, 1.04 wide. Legs: I, femur 0.48, patella 0.20, tibia 0.30, metatarsus 0.14, tarsus 0.38, total 1.50; II, 0.42, 0.18, 0.28, 0.12, 0.34, 1.34; III, 0.30, 0.14, 0.22, 0.12, 0.30, 1.08; IV, 0.40, 0.14, 0.28, 0.14, 0.32, 1.28. Epigynal plate with very dark portions surrounding the genital openings and sinuous posterior margin. Spermathecae small, ducts "S" shaped. (Figs. 5–6).

Anapisona bordeaux Platnick & Shadab

Figs. 7–14

Anapisona bordeaux Platnick & Shadab 1979: 3, figs. 22, 23 (male holotype from Bordeaux Moun-



Figures 7–15.—*Anapisona bordeaux* Platnick & Shadab, male, body: 7. dorsal view; 8. lateral view; palp: 9. prolateral view; 10. retrolateral view; female, body: 11. dorsal view; 12. lateral view; epigynum: 13. dorsal view; 14. ventral view. Scale = 0.25 mm.

tain, St. John, United States Virgin Islands, 17 December 1965, deposited in America Museum of Natural History, New York, not examined).

Material examined.—BRAZIL: *Rio Grande do Sul*: 1 ♂, 1 ♀, São Francisco de Paula, Centro de Estudos e Conservação da Natureza Pró-Mata (29°27'/29°35'S, 50°08'/50°15'W, 500 m), 1999, J. Ketterl (MCTP 13006); 1 ♀, with same data (IBSP 34625).

Diagnosis.—The female of *A. bordeaux* is distinguished from other *Anapisona* females by the coiled copulatory ducts, transversally disposed to the lateral side of spermathecae (Figs. 13–14).

Description.—*Male*: Described by Platnick & Shadab (1979). The male palp of the Brazilian specimens is illustrated in Figs. 9–10. Carapace with deep fovea (Fig. 8). Abdomen with dorsal scutum invaginated distally (Fig. 7).

Female: Carapace and sternum maroon, strongly sclerotized. Abdomen dark brown, with a few lighter areas and four pairs of sclerotized small spots at dorsum (Fig. 11); dorsal scutum absent; lateral and posterior portion of the abdomen remarkably wrinkled (Fig. 12). Carapace with deep round fovea (Fig. 11). Tibia I with 1 prolateral and 1 re-

trolateral distal cusp and 1 prolateral cusp at middle. Measurements. Total length 1.92. Carapace 1.15 long, 0.75 wide, 0.60 high. Abdomen 1.30 long, 1.05 wide. Legs: I, femur 1.07, patella 0.40, tibia 0.85, metatarsus 0.42, tarsus 0.62, total 3.36; II, 0.77, 0.35, 0.57, 0.35, 0.55, 2.59; III, 0.52, 0.27, 0.37, 0.27, 0.42, 1.85; IV, 0.70, 0.25, 0.47, 0.27, 0.47, 2.14. Epigynum with large spermathecae separated by their diameter (Figs. 13, 14).

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SPIDER WEBS AS HABITAT PATCHES—THE DISTRIBUTION OF KLEPTOPARASITES (*ARGYRODES*, THERIDIIDAE) AMONG HOST WEBS (*NEPHILA*, TETRAGNATHIDAE)

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ABSTRACT. Most adult golden orb weavers (*Nephila clavipes*) have kleptoparasites of the genus *Argyroides* in their webs. The kleptoparasitic load correlates positively with web size. Clustered (interconnected) webs have a more predictable number of kleptoparasites than do solitary webs, but there is no difference in the mean number of kleptoparasites between the two. From the view of the kleptoparasite, host webs are habitat patches or islands. Isolated webs show characteristics of small patches, where web size is a poor indicator of kleptoparasite number and variation is high. The distribution of kleptoparasites in clustered webs, on the other hand, seems to fit the “ideal free distribution” where web size nearly entirely predicts kleptoparasitic load. Thus clustered webs, as a habitat patch, are more than merely the combination of their parts. The predictability of kleptoparasite load in clustered webs may be a function of the stability (longevity) of those habitat patches, and ease of colonization, as neighboring webs act as sources.

Keywords: Habitat islands, habitat stability, ideal free distribution, orb web, patch connectivity

Obligatory kleptoparasites of the genus *Argyroides* Simon 1864 are completely dependent on their host webs (Kullmann 1959; Vollrath 1987; Cangialosi 1990; Miyashita 2001); from the perspective of the kleptoparasite, host webs are thus natural habitat patches, or islands. Unlike islands, however, individual host webs are often interconnected, which adds another dimension to the system. Viewed as habitat patches, host web size and kleptoparasite number should be correlated. The isolation, or clustering, of webs should affect the distribution of kleptoparasites among webs. Interconnectedness should facilitate the movement (immigration and emigration) of kleptoparasites between webs. And, ease of immigration/emigration, together with relative longevity of clustered webs, should result in either higher or more stable kleptoparasite load compared to solitary webs.

This study is intended to examine the general correlation (if any) between *Nephila clavipes* (Linnaeus 1767) host orb size and *Argyroides* kleptoparasite load, and specifically, if and how the kleptoparasitic load of interconnected (clustered) webs differs from other webs. I ask three main questions: is there a correlation between orb size and kleptopara-

site number? Is a cluster of interconnected webs equivalent to a gigantic solitary web? Does the distribution of kleptoparasites in host webs appear to fit the ideal free distribution model, as suggested by Elgar (1993)?

Many authors have studied the biology of kleptoparasitic *Argyroides* and its interaction with its hosts (see Elgar 1993 for review), yet understanding of the distribution of kleptoparasites among host webs is fragmentary. Cangialosi (1990) showed a strong correlation between social *Anelosimus eximius* (Keyserling 1884) web size and the number of *Argyroides ululans* O. P.-Cambridge 1880 kleptoparasites residing in them. She attributed this in part to the stability and longevity of the larger colonies. Rypstra & Binford (1995) found that the number of commensal *Philoponella republicana* (Simon 1891) was correlated with web size of its social *A. eximius* host, and that *P. republicana* was more common in social *A. eximius* host webs than in solitary host webs of *Architis* sp. Smith Trail (1980) showed, similarly, that colonies of *Philoponella oweni* (Chamberlin 1924) had higher numbers of *Argyroides ficitium* (Hentz 1850) kleptoparasites than did solitary *P. oweni* webs. Only a few studies have demonstrat-

ed such correlations in *Nephila* Leach 1815 webs. Robinson & Robinson (1973) found that adult *Nephila pilipes* (Fabricius 1793) had more kleptoparasites than did juveniles. Elgar (1989) showed a relationship between host size and kleptoparasitic load (note that host size and orb size are strongly correlated (Witt et al. 1968; Grostal & Walter 1999)), and that clustered webs suffered a higher parasitic load than did solitary webs of *N. edulis* (Labillardière 1799) in Australia. Grostal & Walter (1999) showed a weak correlation between *Nephila plumipes* (Latreille 1804) web size (also in Australia) and kleptoparasite number, but contrary to Elgar (1989), they found no special association between web aggregation and kleptoparasitic load.

This paper reports on *Argyrodes* kleptoparasites in the webs of a fourth *Nephila* species, *N. clavipes* (Linnaeus 1767), in Costa Rica. I look at the data from a different angle (regression variance), and in light of these results I propose a reinterpretation of the results of previous studies.

METHODS

The study was undertaken during the dry season, over a seven day period in February 2001 at Cabo Blanco Absolute Reserve, and three day period in March 2002, in Manuel Antonio National Park, both in Puntarenas Province, on the pacific coast of Costa Rica. Both study sites are in fairly open coastal humid tropical forest. The area has approximately 1400 mm annual rainfall, spread mostly over May–September, but with a dry season between January and April. All observations and data collecting were made from 0900–1700 h.

To assess the distribution of kleptoparasites among host webs, *N. clavipes* webs were located along trails and in the forest within the reserves. For every web encountered, I recorded the owner's size (body length in mm, excluding legs) and developmental status (adult/juvenile based on epigynal appearance), the orb size (height x width of orb in cm) and the number of kleptoparasites occupying each web, including its associated barrier web. Each orb was measured in the same way whether in a cluster or solitary. A web is classified as "clustered" if its structural threads attached to the threads of another *Nephila* web. Solitary webs are any webs that do not

physically touch other webs. The distance to the nearest web was not measured exactly, but was never less than one meter. I used linear regression to examine the relationship of web size and kleptoparasite numbers, both for the pooled data and for clustered and solitary webs separately. I used a preliminary model 'homogeneity of slopes' test to determine the homogeneity of the regression slopes. As homogeneity was rejected, an ANCOVA was not performed. To test if web size can explain kleptoparasite load equally in solitary and clustered webs I compared the variance of kleptoparasite load in clustered versus solitary webs, using a F-test. I used a t-test to compare the mean numbers of kleptoparasites per orb area between clustered and solitary webs.

I assigned a number to each of the *Nephila* webs encountered, thereby establishing a transect of webs which were then used for observations and experiments. Webs were chosen on this transect by randomly picking numbers, alternatively for the two parts of this study, without replacement (so that no single web could be involved in both experiments). To obtain basic information on the distribution of kleptoparasites *within* host webs, in particular during orb reconstruction, 15 *Nephila* webs were monitored over a 6 day period for a total of 40 observation hours. The data collected was not quantitative, I visited the chosen webs haphazardly, and noted the whereabouts (in barrier web or in orb) and movements of the kleptoparasites, and anecdotal information about the behavior of the kleptoparasites as well as their interaction with the host were also noted. To compare the rates of colonization in clustered and solitary webs, I removed kleptoparasites from 10 solitary and 10 clustered webs. If more than one web was chosen from a particular cluster, I removed the kleptoparasites of only a single web daily, consecutively over the six day period. I counted the number of kleptoparasites in these webs the day after their removal and calculated the difference in re-colonization rates using a two sample t-test.

Voucher specimens from this study are deposited in the arachnological collection of the National Museum of Natural History, Smithsonian Institution.

RESULTS

I encountered 70 *Nephila* webs (48 solitary webs, 22 clustered, in a total of 7 clusters)

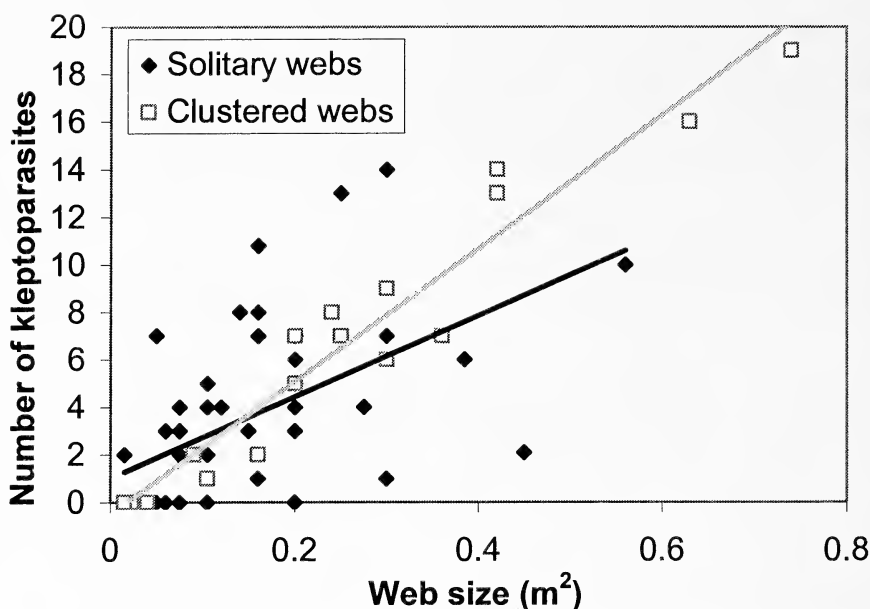


Figure 1.—Kleptoparasite load is correlated with web size in both solitary and clustered *Nephila clavipes* webs in Costa Rica. In clustered webs the number of kleptoparasites is nearly entirely linearly predicted by web size ($r^2 = .94$). On the other hand, solitary webs have a highly variable number of kleptoparasites ($r^2 = .29$).

containing close to 300 kleptoparasites. The orbs of solitary webs ranged in size from 0.015–0.56 m², while the orbs of webs that were part of a cluster ranged from 0.015–0.77 m². In either case, I found kleptoparasites only in webs larger than 0.04 m² (i.e. about 20 × 20 cm). The largest web encountered (90 × 80 cm, located in the center of a cluster) had the highest number of kleptoparasites, 18.

Two *Argyrodes* species were identified: *A. elevatus* Taczanowski 1873 of the “*A. argyrodes*” group and *A. caudatus* (Taczanowski 1874), of the “*A. cancellatus*” group (Exline & Levi 1962). Kleptoparasitic load increased with web size, pooling all data ($r^2 = 0.61$, $F = 109.2$, $df = 68$, $P < .001$, $n = 70$) (Fig. 1). Looking at clustered and solitary webs separately, web size explained nearly all the variance in clustered webs ($r^2 = 0.94$, $F = 310.2$, $df = 20$, $P < .001$, $n = 22$) but much less so in solitary webs ($r^2 = 0.29$, $F = 19.8$, $df = 46$, $P < .001$, $n = 48$). The homogeneity of the regression line slopes is rejected ($S^2 = 42.506$, $F = 5.861$, $df = 1$, $P = 0.018$). The difference in variance in kleptoparasitic load in clustered ($S^2 = 2.1$) and solitary ($S^2 = 9.5$) webs is significant ($F(2)_{20,46} = 4.5$, $P < .01$). There was no difference in the mean number

of kleptoparasites per web area between clustered (18.5 kleptoparasites/m², $SD = 13.3$) and solitary (23.1 kleptoparasites/m², $SD = 26.4$) webs ($t = 0.77$ $df = 68$, $P = 0.443$).

The kleptoparasites, when not foraging, spent most of their time in the host barrier web, which provides a haven outside the monitoring range of the host. In two instances *Nephila* orb reconstruction was observed and in both cases the kleptoparasites were observed maintaining an association with that particular host. As *Nephila* rebuilt its orb the kleptoparasites resided in the unaltered barrier web, and no emigration was observed in these two cases. The fresh orb was connected to the old barrier web, and after its completion the kleptoparasites rebuilt their association lines. Most of the kleptoparasites were only ever seen entering a single host web, even if that host web was connected to another. Yet, a few spiders did have silk lines leading to two host webs (counted only once and assigned to the nearest web), and thus could “monitor” more than one web at a time and forage in either (see also Whitehouse & Jackson 1993). All *Argyrodes* instars occurred in host webs, and both species were observed mating in the host bar-

rier web. *Argyrodes* egg sacs were found hanging from the *Nephila* barrier web.

A day after removal of kleptoparasites two of the 10 webs in clusters had three kleptoparasites, five webs had two and three webs had one, while seven of the 10 solitary webs had zero and three had one kleptoparasite, respectively. The re-colonization rates of clustered versus solitary webs differed ($t = 5.737$ $df = 18$, $P < .001$).

DISCUSSION

As in *N. edulis* (Elgar 1989) and *N. plumipes* (Grostal & Walter 1999), the number of *Argyrodes* kleptoparasites correlates positively with web size in *N. clavipes* (Fig. 1). If in clusters, orb size explained nearly all variation in kleptoparasite number whereas if solitary, orb size explained much less of the variation. Although the regression slope of clustered webs is steeper, solitary webs did not have lower mean number of kleptoparasites (unlike *N. edulis*, see Elgar 1989).

Elgar (1993) suggested that the distribution of kleptoparasites among host webs in some cases seems to follow the 'ideal free distribution' (Milinski & Parker 1991). The ideal free distribution model states that for a given population size k , there exists a distribution of individuals such that the "suitabilities" derived from each habitat are equal and hence stable (Krebs 1994). If all individuals are "free" to move to alternate patches, then "ideally" each will find the place that maximizes its gain.

The results obtained here suggest that ideal free distribution may only be an appropriate model in the case of clustered webs. It seems that the parasite load for host webs in clusters has an optimal upper limit and the low variance in kleptoparasite numbers suggests that *N. clavipes* webs in clusters are generally near or at that limit. Miyashita (2001) demonstrated that in *Nephila clavata* L. Koch 1878 webs in Japan, the removal of *Argyrodes flavescens* (O. P.-Cambridge 1880) kleptoparasites resulted in a remarkably rapid influx of other individuals of that and another *Argyrodes* species. He interpreted this as evidence for strong inter- and intraspecific competition for limited host web space. Grostal & Walter (1999:557, fig. 4) also concluded that orb diameter imposed an upper limit on kleptoparasite numbers. Furthermore, clustered webs that were

cleaned of kleptoparasites in this study regained them more rapidly than did solitary webs.

Kleptoparasites in web clusters can easily relocate to a web that provides more prey (i.e. the ideal free distribution). An "extinction" event (disappearance of a kleptoparasite) is short-lived because the neighboring webs act as sources. Web clusters are, in addition, relatively long lived habitat patches, increasing the probabilities of colonization by kleptoparasites. Solitary webs, on the other hand, are more like islands. They may first of all never reach an upper limit because they are relatively short lived, immigration is more stochastic, and they will experience higher rates of extinction (a solitary *Nephila* death will result in total extinction or emigration, whereas a *Nephila* death in a web cluster will result in only partial extinction/emigration from the cluster). Second, some solitary webs have a higher number of kleptoparasites per web area than any one in a cluster. This may be a result of a greater "risk" of emigrating from isolated webs and difficulties of finding new ones— isolation makes reaching an ideal distribution harder.

Patch connectivity thus seems to be of great importance in the distribution of kleptoparasites among *Nephila* webs. A web cluster is not merely equivalent to a gigantic solitary web; it is rather a community of distinct webs, each potentially experiencing multiple extinctions and colonizations of kleptoparasites.

Grostal & Walter (1999) found their results to conflict with those of Elgar (1989) and suggested that the distribution of kleptoparasites might be more random than Elgar had concluded. The findings of this study agree with Elgar's (1989) that there is a difference in kleptoparasitic load of clustered and solitary webs. However, the difference seems to be one of stability, therefore comparing simply the mean number of kleptoparasites may not be sufficient to detect those differences. Neither Elgar nor Grostal & Walter considered the regression variance in host web occupation, and thus could not have discovered the patterns reported here. Furthermore, both the current study and that of Elgar were "snapshots in time", done over a period of a few days, whereas that of Grostal & Walter took place over different seasons. Vollrath (1987) and Higgins & Buskirk (1998) found large sea-

sonal fluctuations in the population sizes of kleptoparasitic *Argyrodes* and their *Nephila* host. Pooling data from different seasons could easily obscure correlations between kleptoparasite load and web size at smaller time scales. Finally, the current study would predict a greater mean number of kleptoparasites in clustered webs if the majority of webs considered were large (see Fig. 1). Elgar (1989) found a very low percentage of webs without kleptoparasites (one out of 92) and a high mean number of kleptoparasites per web (10, versus e.g. 4.2 in the current study) suggesting that his study may indeed have been biased towards larger webs. Thus, reanalysis of the data of these previous studies is likely to reveal more general and congruent patterns, the presumed conflict being more apparent than real.

The structural complexity and longevity of *Nephila* web clusters may explain, at least partially, the greater stability of kleptoparasite populations in them, versus the shorter lived solitary webs. A growing amass of evidence indicates that kleptoparasites greatly prefer complex, long-lived, webs (e.g. *Anelosimus* Simon 1891, *Argiope* Audouin 1826, *Cyrtophora* Simon 1864, *Diplura* C.L. Koch 1850, *Stegodyphus* Simon 1873, *Tengella* Dahl 1901 and *Nephila*), to simpler webs taken down frequently (see Elgar 1993 for review; Miyashita 2002). Given that *Argyrodes* kleptoparasites can significantly and detrimentally affect their hosts (Vollrath 1980; Rypstra 1981; Elgar 1989; Grostal & Walter 1997; Higgins & Buskirk 1998) it is tempting to speculate that frequent web renewal may represent an adaptation against kleptoparasitism. Cause and effect in this case may be hard to tease apart, as many other factors affect web duration (e.g. predation by sphecids wasps). The lack of kleptoparasites in "daily webs" seems nevertheless beneficial and further work might profitably explore the idea.

Nephila webs are not only insect snares, but also discrete habitat islands hosting a dynamic community of kleptoparasitic spiders dependent upon them. Available studies have all shown a correlation between patch (web) size and population size, and the current study shows an increase in population stability with patch connectivity—a cluster of small webs is a more predictable (stable) habitat patch than a large solitary web. These characteristics

epitomize general ecological models, such as island biogeography (MacArthur & Wilson 1967) and metapopulation biology (Hanski 1999). In order to test such models, future studies should include additional factors, e.g. absolute distances between webs, number of webs per cluster, barrier web size, phenology of both host and kleptoparasites, and the patterns of migration between host webs. For such studies *Nephila* webs are ideal as both their relative longevity (thus habitat stability) (e.g. Wiehle 1927; Lubin 1983; Foelix 1996), and the extensiveness of their mesh-like barrier webs, may increase kleptoparasitism (Whitehouse 1988; Cangialosi 1990, 1997; Grostal & Walter 1999; Miyashita 2002). The barrier web provides a safe substrate for the kleptoparasites from which to monitor the host web (e.g. Vollrath 1979a, 1979b; Whitehouse 1986; Cangialosi 1990), it makes the orb three dimensional, which may facilitate group living (Krafft 1979; Agnarsson 2002), and it allows the kleptoparasites to stay associated with the host during orb reconstruction.

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SPIDER FAUNA OF SUGAR MAPLE AND WHITE ASH IN NORTHERN AND CENTRAL NEW YORK STATE

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ABSTRACT. The purpose of this study was to identify spiders associated with foliage of sugar maple, *Acer saccharum* Marsh. and white ash, *Fraxinus americana* L., and to investigate their distribution and relative abundance within the crowns of these two northern hardwoods. Spiders were collected during June through August 1995 from the lower and mid-crowns of ten dominant/codominant sugar maples, five white ash and understory sapling and herbaceous foliage ≤ 2 m from the ground in a northern hardwood stand in Cortland County New York. These samples were compared for differences in species composition and density (number/25 leaf-clusters; number/100 g dry leaf weight). The spider fauna obtained from this intensive sample was compared to that of an extensive, 20-year survey from the mid-crown of sugar maple in 15 northern hardwood stands in northern New York (St. Lawrence and Lewis Counties). The intensive overstory collection (1995) from maple provided 694 specimens (7 families, 11 genera, 13 species). The dominant families were Philodromidae (43%) and Theridiidae (26%). The most abundant species were *Philodromus rufus* Walckenaer 1826 and *Enoplognatha ovata* (Clerck 1757). Sugar maple averaged 2.6 ± 0.6 spiders/25 leaf-clusters and $14.2 \pm 0.6/100$ g of foliage. Density of dominant taxa and total numbers did not differ significantly ($\alpha = 0.05$) between crown positions. Significantly fewer hunters/100 g leaf weight occurred on the distal half of mid-crown branches compared to the basal half. Hunters were the dominant foraging guild in terms of both numbers (65%) and number/100 g leaf weight (56%). One hundred twenty four specimens were obtained from white ash (7 families, 9 genera, 9 species). Density on ash averaged $2.6 \pm 1.3/100$ g leaf weight and *P. rufus* and *Araniella displicata* (Hentz 1847) were the most abundant species. Significantly fewer spiders occurred on white ash compared to sugar maple ($14.2 \pm 0.6/100$ g of foliage). The extensive sample provided 712 specimens consisting of 12 families, 27 genera and 40 species. The most abundant species recovered was *Pelegrina proterva* (Walckenaer 1837). The web spinner, *E. ovata* was the most common species recovered from understory foliage (96% of 763 specimens).

Keywords: Spider diversity, community structure, biodiversity

Sugar maple, *Acer saccharum* Marsh., is important to the ecology and economic value of many northern hardwood forests. In recent decades, its abundance has steadily increased relative to associated species in this forest type (Allen 1996), most likely due to its silvical characteristics (Godman et al. 1990) and forest management practices (Nyland 1992). The major defoliators of sugar maple (Houston et al. 1990; Martineau 1984) and their insect parasitoids and predators (e.g., Allen 1972, 1976a, 1979; Côté & Allen 1973) are well known, but only two studies have examined the spider fauna on this tree species

or in a northern hardwood forest where it was a major component. These arachnids are potential natural control agents. The first step in elucidating their significance in this respect is to identify the species present in tree crowns and determine their relative abundance. Uetz and Dillery (1969) collected spiders in a residential area of Albion, Michigan from the lower crowns of sugar maple during the fall. Throughout the growing season of 1961 through 1964, Drew (1967) sampled for spiders in the herb-shrub and leaf litter strata of a beech-maple forest on Beaver Island, Michigan.

The primary objective of this study was to identify the arboreal spiders associated with sugar maple sampled in northern New York State (St. Lawrence and Lewis Counties) an-

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nually from 1975 through 1995 and compare these species and their relative densities with those recovered in an intensive, one-year (1995) sample in a central region of the state (Cortland County). Secondary objectives were: to determine if spider fauna and spider density varied with crown position in sugar maple and white ash, *Fraxinus americana* L., a common associate of maple in northern hardwood forests; to compare the species composition of the spider community on understory foliage with that found in overstory crowns and to determine the relative abundance of web spinning and hunting spiders in these habitats.

METHODS

From June–August 1995, sampling for spiders in north-central New York took place at Heiberg Forest (Cortland County), a property of the State University College of Environmental Science and Forestry. The site encompassed approximately one hectare and the overstory was predominantly sugar maple, with white ash as a secondary species. The stand also contained black cherry (*Prunus serotina* Ehrh.), quaking aspen (*Populus tremuloides* Michx.) and red maple (*A. rubrum* L.).

Understory vegetation comprised mainly sugar maple and white ash regeneration, along with scattered red maple, Virginia creeper (*Parthenocissus quinquefolia* Planch.), poison ivy (*Rhus radicans* L.), blue cohosh (*Caulophyllum thalictroides* (L.) Michx.), trillium (*Trillium* sp.), thistles (*Cirsium* sp.), touch-me-not (*Impatiens* sp.) and asters (*Aster* sp.). The soil at this site is classified as Mardin channery silt loam, medium-textured, strongly acidic and moderately well drained (Seay 1961).

Spiders were collected from northeast and southwest quadrants of the lower and middle third of the crowns (foliated portion) of ten sugar maples. Sample trees had a mean diameter at breast height (dbh = diameter at 1.4 m from the ground) of 46.4 ± 1.1 cm (SE) and a mean height of 22.4 ± 1.1 m and five white ash (mean dbh = 20.7 ± 2.4 cm; mean height = 17.4 ± 2.3 m). Samples were distributed in this manner to determine if spider density varied with crown position. It was assumed the two aspects and two crown levels sampled represented habitats where relevant differences in temperature and humidity were

likely to occur which, in turn, may have influenced spider distribution (Pointing 1966). Two branches were removed from each sampled quadrant and crown level. Each branch was then divided into distal and basal halves, each half was bagged separately and brought to the laboratory for processing. Therefore, there were 160 sample units for sugar maple (2 aspects \times 2 crown levels \times 2 branches \times 2 branch sections \times 10 trees) and 80 sample units for white ash (2 aspects \times 2 crown levels \times 2 branches \times 2 branch sections \times 5 trees). Sample branches were selected arbitrarily, cut at the base with a hand saw and carefully lowered onto a drop cloth. The following information was obtained for each branch section: length (m), basal diameter (cm), number of leaves, dry leaf weight (g), number of leaf-clusters (sugar maple only) and number of spiders.

Within a crown level, spider numbers from both quadrants (NE, SW) were averaged to compensate for possible variation associated with spider movements due to diurnal fluctuation of physical variables (Pointing 1966) or prey movement (Nyffeler et al. 1994). Spider densities for each sugar maple branch section (distal half, basal half) were recorded as numbers per 25 leaf-clusters to weight samples for differences in foliage quantities. For both sugar maple and white ash, spider densities were also expressed as numbers per 100 g of dry leaf weight. This compensated for differences in foliage biomass and facilitated comparison of spider densities between the two tree species.

Spiders were hand collected from the understory by starting at one end of the site, walking in a straight line to the opposite side and searching all foliage within 2 m of the ground. At the opposite end of the transect, walking direction was reversed and the site was traversed a second time parallel to the first line. Approximately 100 transects spaced at 1 m intervals were required to examine understory foliage within the 1 hectare site.

Spiders were identified by the senior author using published keys of Comstock (1948) Dondale (1978, 1982) Kaston (1948, 1978) and Levi (1957, 1963); and by using reference collections. Determinations of representative species were confirmed by D.T. Jennings. Most females were identified by external examination of the epigynum; however, for *Pe-*

legrina spp. it was necessary to dissect and examine the internal morphology of this structure. Males were identified by examining palpal morphology. Adult spiders in good condition were identified to species, damaged individuals to family. Recognizable juveniles were identified to species, otherwise they were identified to genus or family. Enumeration of spider taxa follows Platnick (1989, 1993, 1997) and Maddison (1996). The entire collection is housed in the invertebrate museum of the Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, New York.

Both the paired *t*-test and 2×2 factorial ANOVA ($\alpha = 0.05$) were employed to analyze within-crown distributions of spiders on sugar maple. Data were tested for homogeneity of variances prior to analyses. The G-test (Sokal & Rohlf 1981) was calculated to compare web spinner *vs* hunter (i.e., all non-web spinners) percentages for sugar maple, white ash, and sugar maple in the understory.

The spider fauna collected in north-central New York during 1995 was compared to a 20-year collection (1975–1995) made by D.C. Allen at 15 sites located in two northern counties of the state (St. Lawrence, Lewis). This extensive sample was made in conjunction with annual monitoring of sugar maple foliage for eggs of the saddled prominent, *Heterocampa guttivitta* (Walker) (Lepidoptera, Notodontidae). For these annual samples, a 1.5 m branch tip was removed with aluminum pole-pruners from the mid-crown level (middle third of the foliated portion of the tree; in these stands, 12–15 m above ground) of each of ten dominant or co-dominant trees. Overall sample size was: 1 branch tip/tree \times 10 trees/site \times 15 sites/yr. \times 20 yrs. = 3000 branches. Additionally, spiders were occasionally collected by hand from the lower crowns ($n = 58$ specimens) of sugar maple. Each year sampling was done during the last week of June or first week of July. Sampled stands represent the northern hardwood forest type; i.e., each consisted of 50% sugar maple, American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton), either singly or in combination (USDA Forest Service 1965). In 1975 tree size (dbh, cm), abundance (trees/ha) of sugar maple and stand density (BA, m²/ha) were similar among all sites

(D.C. Allen, unpubl.). In 1995, stand density averaged 22.0 ± 3.0 (SE) m²/ha, 79% of which was sugar maple (range 35–98%). For six of these stands measured again in 1997, diameter of sugar maple ranged from 30.6 ± 1.6 cm to 41.6 ± 2.4 cm. All stands are second growth, 100–110 years old and have a history of intensive management for wood products or sap production.

For the 20-year study, numbers of spiders are reported as total collected and each species as percent of total spiders collected compared to the 1995 study that focused on spiders per unit of foliage. In most cases spider numbers cannot be compared statistically; however, the spider complex recovered in the 20-year sample provided an opportunity to compare dominant species, genera, and families with material obtained during the more intensive short-term study (1995) in a different geographic location.

RESULTS

Spiders collected from sugar maple in 1995 comprised 694 specimens, representing 7 families, 11 genera and 13 species (Table 1). Only 32 specimens (0.05%) were adults. Principal families were Philodromidae (47%) and Theridiidae (26%). The Clubionidae, Araneidae, Salticidae, Linyphiidae, and Tetragnathidae together accounted for 28% of the collection. Numerically dominant species were *Philodromus rufus* Walckenaer 1826 (47%) and *Enoplognatha ovata* Clerck 1757 (22%). Their dominance based on relative density (spiders/100 g of leaf weight) was: *P. rufus* (38%), and *E. ovata* (30%). For example, if there were 14 spiders per 100 g of leaf weight, approximately five (38%) were philodromids.

An average of 2.6 ± 0.6 (SE) spiders/25 leaf-clusters and 14.2 ± 0.6 spiders/100 g of leaf weight occurred on the 160 branch sections from sugar maple. Neither the 2×2 factorial ANOVA (Table 2) nor paired *t*-tests revealed significant differences in number of spiders/25 leaf-clusters or number of spiders/100 g leaf weight for two sugar maple crown positions (mid-*vs* lower crown), total numbers (both guilds combined), dominant taxa (family, genus and species), or numbers of web spinners. There was a significant ($P = 0.02$) interaction for numbers of hunters/100 g leaf weight in mid-crown distal branch sections; however, the main effects were not significant

Table 1.—Species and numbers of spiders collected from sugar maple at Tully, Cortland County, New York, 1995.

Spider taxa	Number of individuals
Theridiidae	
<i>Enoplognatha ovata</i> (Clerck 1757)	150
<i>Theridion murarium</i> Emerton 1882	12
<i>Theridion</i> sp.	18
(family only)	2
Linyphiidae	
<i>Ceraticelus</i> sp.	5
<i>Neriene</i> sp.	8
Araneidae	
<i>Araneus nordmanni</i> (Thorell 1870)	1
<i>Araneus</i> sp.	10
<i>Araniella displicata</i> (Hentz 1847)	32
<i>Cyclosa conica</i> (Pallas 1772)	1
Tetragnathidae	
<i>Tetragnatha laboriosa</i> Hentz 1850	1
<i>Tetragnatha</i> sp.	1
Clubionidae	
<i>Clubiona canadensis</i> Emerton 1889	94
<i>Clubiona obesa</i> Hentz 1847	3
<i>Clubiona</i> sp.	7
Philodromidae	
<i>Philodromus rufus</i> Walckenaer 1826	296
<i>Philodromus vulgaris</i> (Hentz 1847)	26
<i>Philodromus</i> sp.	1
Salticidae	
<i>Pelegrina proterva</i> (Walckenaer 1837)	2
<i>Pelegrina</i> sp.	24
Total	694

(mid- vs lower crown, $P = 0.31$; and basal vs distal branch sections, $P = 0.43$). Spiders/100 g of leaf weight and spiders/25 leaf-clusters were highly correlated (Pearson-Product Moment) with each other for both web spinners ($r = 0.99$) and hunters ($r = 0.97$). The crown level-branch position interaction for hunting spiders/25 leaf-clusters was close to significance ($P = 0.06$), and the correlation between crown level and aspect was very high ($r = 0.97$). For the mid-crown level of sugar maple, significantly ($P = 0.06$, Table 2) fewer hunters/100 g leaf weight occurred on distal branch sections (mean = 3.0 ± 1.7) compared to basal sections (10.5 ± 3.2) (Table 3). Conversely, density of web spinners was similar between branch positions within both crown levels (Table 3). Hunters were the dominant

foraging guild based on total spiders (65%) and on spiders/100 g of leaf weight (56%). Understory samples produced 763 specimens (98% juveniles) representing the Theridiidae, *Enoplognatha ovata* (Clerck 1757), $n = 737$; *Theridion* sp., $n = 2$; Araneidae, *Araniella displicata* (Hentz 1847), $n = 2$; *Cyclosa conica* (Pallas 1772), $n = 14$; Clubionidae, *Clubiona obesai* Hentz 1847, $n = 1$, *Clubiona* sp., $n = 3$; Philodromidae, *Philodromus rufus* Walckenaer 1826, $n = 3$ and *Philodromus* sp., $n = 1$. The principal understory species, *E. ovata*, comprised 96% of the total collection, and weighted guild composition in favor of web spinners (98%).

One hundred twenty-four specimens were recovered from white ash and were represented by the Theridiidae, *Theridion murarium*

Table 2.—Results of ANOVA (2 × 2 factorial) for main effects (crown level, branch position) and interaction effects (crown level vs branch position) for spider densities on sugar maple at Tully, Cortland County, New York, 1995. 1 = mid-crown vs lower crown; 2 = basal branch section vs distal branch section; 1, 2 = interaction of crown levels and branch position. Significance ($\alpha = 0.05$).

Variable	Effects	Spiders/25 Leaf-clusters		Spiders/100 g Leaf weight	
		P	F	P	F
Total Spiders	1	0.45	0.59	0.21	1.70
	2	0.38	0.79	0.36	0.88
	1, 2	0.12	2.43	0.36	0.85
Web Spinners	1	0.40	0.73	0.37	0.84
	2	0.20	1.69	0.16	2.09
	1, 2	0.76	0.09	0.76	0.09
Hunters	1	0.31	1.04	0.31	1.04
	2	0.35	0.88	0.43	0.63
	1, 2	0.06	3.73	0.02	6.43

Emerton 1882, $n = 1$; Linyphiidae, *Ceraticelus* sp., $n = 2$; *Drapetisca* sp., $n = 1$; Araneidae, *Araneus* sp., $n = 1$, *Araniella displicata* (Hentz 1847), $n = 40$; Clubionidae, *Clubiona* sp., $n = 5$; Thomisidae, *Misumena vatia* (Clerck 1757), $n = 1$; Philodromidae, *Philodromus rufus* Walckenaer 1826, $n = 42$; Salticidae, *Pelegrina proterva* (Walckenaer 1837), $n = 29$ and *Pelegrina* sp., $n = 1$. Spider density on white ash averaged 2.6 ± 1.3 (SE)/100 g of leaf weight. Only 4 (0.03%) individuals were adults; most were juveniles of *P. rufus* and *Araniella displicata* (Hentz 1847). *Philodromus rufus* accounted for 34% and *A. displicata* 32% of the total spiders collected from white ash. Densities per 100 g of leaf weight for these two species were 39% and 30%, respectively. Hunters were the dominant foraging guild on white ash, both in terms of total specimens (63%) and numbers/100 g of leaf weight (60%).

White ash averaged significantly fewer ($t = 2.184$, $P = 0.03$, $df = 58$) spiders per 100 g

of foliage biomass (2.6 ± 1.3) than sugar maple (14.2 ± 0.6). Sugar maple branches (1 m long) averaged 53.3 ± 3.3 g of leaf weight compared to 71.7 ± 7.1 g for white ash ($t = 2.452$, $P = 0.02$, $df = 58$) branches of the same length. However, sugar maple had significantly ($t = 8.031$, $P = 0.0001$, $df = 58$) more leaves per 1 m branch (276.8 ± 17.9) than white ash branches of the same length (93.9 ± 10.5 leaves). Each white ash leaf consists of 5–9 leaflets, which most likely accounts for the greater average leaf weight.

Only 712 spiders were recovered while sampling sugar maple foliage yearly from 1975–1995. The collection represented 12 families, 27 genera and 40 species (Table 4). Most were adults (455 or 64%). Numerically dominant families were Salticidae (32%), Philodromidae (21%) and Theridiidae (12%). The salticid *Pelegrina proterva* (Walckenaer 1837) (25%) was the primary species recovered. Hunters were the dominant foraging guild, accounting for 64% of the collection.

Table 3.—Mean (\pm S.E.) number of spiders/100 g of leaf weight for two branch positions in the mid- and lower crown of sugar maple ($n = 10$ trees), Tully, Cortland County, New York, 1995.

Spider group	Branch position	Crown level		Crown levels combined
		Lower	Middle	
Webspinners	Basal Half	10.7 ± 8.1	2.1 ± 0.9	6.4 ± 4.1
	Distal Half	6.9 ± 5.0	0.9 ± 0.6	3.9 ± 2.5
	Branch Positions Combined	8.8 ± 4.7	1.5 ± 0.5	—
Hunters	Basal Half	12.1 ± 5.6	10.5 ± 3.2	11.3 ± 3.1
	Distal Half	7.9 ± 3.8	3.0 ± 1.7	5.5 ± 2.1
	Branch Positions Combined	10.0 ± 3.3	6.8 ± 2.0	—

The ability to estimate population densities of arboreal spiders is important for assessing the dynamics of spiders as predators of folivores in forested ecosystems. To determine the relationships between certain tree characteristics and leaf-cluster numbers, Allen (1976b) conducted a dimension analysis of sugar maple in Tully, New York (Cortland County). A leaf-cluster (all leaves derived from a single bud) is the unit of habitat occupied by many insect folivores and spiders. He found that the total number of leaf-clusters/tree can be estimated by dbh^2 or, a combination of tree diameter, height and crown size (length, width). For example, in two separate samples (1970, $n = 18$ trees; 1971, $n = 16$ trees) there was a significant positive correlation ($r = 0.90$, 1970; $r = 0.93$, 1971) between dbh^2 and the total number of leaf-clusters for overstory sugar maples 18–38 cm in diameter. Using a regression derived from the 1971 sample (Allen, unpub. data) ($Y = 574.6 + 87.6 \text{ dbh}^2$), a sugar maple 14.5 inches (36.8 cm) dbh contains approximately 18,993 leaf-clusters. Assuming that spider density (spiders/25 leaf-clusters) is similar among overstory sugar maples; total leaf-cluster numbers increase or decrease in a predictable manner relative to tree diameter and 2.6 spiders/25 leaf-clusters was representative of the entire maple crown; then a 36–37 cm diameter sugar maple at Heiberg Forest in 1995 contained approximately 1,975 spiders.

DISCUSSION

Previous investigations of spiders associated with forest trees in North America have concentrated mainly on conifers, and have employed a diverse array of sampling methods (Table 5). Relatively few studies have been published on spiders associated with broad-leaved trees. Additionally, spider guild ratios have been based on total number collected, not on population numbers or densities expressed as number per unit of habitat (e.g., spiders/leaf-cluster, spiders/100 g foliage). To be most meaningful, sample ratios of spider guilds should reflect the percent of the estimated total per specific unit. For example, if for the 1995 study the ratio of hunters (65%) to web spinners (35%) is based on total spiders collected, the result is approximately 2:1 in favor of hunters. However, a ratio determined on the basis of spiders/per 100 g of leaf

weight approximates a 1:1 ratio (hunters 56% and web spinners 44%) and more accurately reflects the relative abundance of these two groups per unit of habitat. Employment of different sampling protocols (e.g., timing, technique) and field conditions, however, may have favored one guild over another (Green 1999).

In the 1995 study, the numerically dominant species on both white ash and sugar maple was the hunter *P. rufus*. This arboreal species does not construct a web, but spins a silken retreat on the underside of a leaf for egg laying. Observations of *P. rufus*, both in the lab and under field conditions, indicated that it is extremely fast and agile compared to other spiders encountered. Although *P. rufus* has limited eyesight (Haynes & Sisojevic 1966), agility and swiftness of movement may contribute to its dominant status. These characteristics enhance predator avoidance, prey capture and protection of eggs. This widely distributed species and three subspecies have been recovered from a variety of coniferous and broad-leaved trees in North America (all references Table 5).

The web spinner *E. ovata* was the most abundant species recovered from understory foliage and comprised 96% of all spiders collected in this stratum. Interestingly, this theriidid was also second in abundance on sugar maple overstory (30%). Previous studies of the araneofauna associated with trees do not report *E. ovata* as a common species (all references Table 5). Reillo and Wise (1988) noted that *E. ovata* frequently occurred on weedy vegetation in Maine. Most likely introduced from Europe (Levi 1957), this species (previously described as three separate species of *Theridion*) has three phenotypes (Kaston 1948). Two forms have red markings on the abdomen, while one form is without red markings. In the 1995 study, only three individuals had red markings in the combined overstory/understory collection ($n = 887$).

Typically, *E. ovata* attaches silken lines to a leaf, draws the threads together and partially folds the leaf. Potential prey enter the fold and, in doing so, get caught in the web. The folded leaf and web are comparable to a hunting spider's retreat. Presumably, the folded leaf provides protection from adverse weather, affords a safe haven for egg laying, and facilitates concealment from predators. Five egg

Table 4.—Families, species and numbers of spiders collected on sugar maple foliage from 1975 through 1995, various localities, northern New York State.

Spider taxa	Number of individuals
Dictynidae	
<i>Emblyna manitoba</i> Ivie 1847	1
<i>E. maxima</i> (Banks 1892)	37
<i>E. sublata</i> (Hentz 1850)	22
<i>Emblyna</i> sp.	12
Amaurobiidae	
<i>Callobius bennetti</i> (Blackwall 1846)	1
<i>Coras</i> sp.	1
Theridiidae	
<i>Enoplognatha ovata</i> (Clerck 1757)	1
<i>Enoplognatha</i> sp.	1
<i>Theridion differens</i> Emerton 1882	3
<i>T. frondeum</i> Hentz 1850	50
<i>T. murarium</i> Emerton 1882	19
<i>T. sexpunctatum</i> (Emerton 1882)	1
<i>Theridion</i> sp.	9
<i>Theridula opulenta</i> (Walckenaer 1841)	1
(family only)	2
Linyphiidae	
<i>Ceraticelus atriceps</i> (O.P.-Cambridge 1874)	3
<i>C. emertoni</i> (O.P.-Cambridge 1874)	2
<i>Helophora insignis</i> (Blackwall 1841)	3
<i>Hypselistes florens</i> (O.P.-Cambridge 1875)	1
<i>Neriene radiata</i> (Walckenaer 1841)	1
(family only)	16
Araneidae	
<i>Araneus marmoreus</i> Clerck 1757	18
<i>Araneus</i> sp.	29
<i>Araniella displicata</i> (Hentz 1847)	1
<i>Araniella</i> sp.	13
<i>Cyclosa conica</i> (Pallas 1772)	1
(family only)	7
Tetragnathidae	
<i>Tetragnatha elongata</i> Walkenaer 1841	1
Agelenidae	
<i>Agelenopsis utahana</i> (Chamberlin & Ivie 1933)	3
Clubionidae	
<i>Clubiona canadensis</i> Emerton 1889	7
<i>C. obesa</i> Hentz 1847	14
<i>C. pygmaea</i> Banks 1892	6
<i>Clubiona</i> sp.	22
(family only)	12
Liocranidae	
<i>Phruotimpus borealis</i> (Emerton 1911)	1
Thomisidae	
<i>Misumena vatia</i> (Clerck 1757)	4
<i>Misumena</i> sp.	4
<i>Misumenops</i> sp.	1
<i>Xysticus</i> sp.	4

Table 4.—Families, species and numbers of spiders collected on sugar maple foliage from 1975 through 1995, various localities, northern New York State.

Spider taxa	Number of individuals
Philodromidae	
<i>Philodromus</i> sp. (aureolus group)	3
<i>P. exilis</i> Banks 1892	6
<i>P. rufus</i> Walckenaer 1826	51
<i>P. vulgaris</i> (Hentz 1897)	4
<i>Philodromus</i> sp.	27
(family only)	56
Salticidae	
<i>E. militaris</i> (Hentz 1845)	4
<i>Evarcha hoyi</i> (Peckham & Peckham 1883)	2
<i>Hentzia mitrata</i> (Hentz 1846)	2
<i>Pelegrina flaviceps</i> Kaston 1973	1
<i>P. montanus</i> (Emerton 1891)	19
<i>P. proterva</i> (Walckenaer 1837)	180
<i>Pelegrina</i> sp.	16
<i>Phidippus whitmanii</i> Peckham & Peckham 1990	1
(family only)	5
Total	712

sacs of *E. ovata* averaged 103.0 ± 18.0 eggs/sac, about six times that observed for *P. rufus* (17.2 ± 2.0 , $n = 5$).

There were no statistically significant differences ($\alpha = 0.05$) in spider densities between the two crown levels or between the two branch positions sampled on sugar maple (Table 3). This apparent lack of statistical differences results from a combination of low means, high variances and frequent zero counts. We believe, however, the data suggest biological differences and recommend that lower crowns should be sampled to obtain a representative picture of the web-spinning fauna associated with sugar maple foliage. Both the mid- and lower crown should be sampled for hunters. Clearly, future studies should use a larger sample size. Variables such as habitat distribution, differences in microclimate and territorial behavior of some species, for example, affect both inter- and intraspecific distributions. Location preferences were not observed for dominant families, genera, or species. Because analyses were based on densities per 100 g of leaf weight, a distal branch section from either the lower or mid-crown level of sugar maple provides a representative sample of the dominant spider taxa present.

Our sample of only 5 white ash trees ($n = 80$ branch positions) provided estimates of spider density per 100 g of leaf weight and information on species composition. The sample was not large enough, however, to provide insight about the within-crown distributions of spider taxa. For total spiders, variances were homogeneous, but there were no significant differences ($P > 0.05$) between crown or branch positions.

There were significantly fewer spiders/100 g of leaf biomass on white ash compared to sugar maple. Sugar maple had a higher average number of leaves per meter of branch length (276.8 ± 17.9) compared to the average number of leaves (each leaf with 5–9 leaflets) on white ash (93.9 ± 10.5), but lower leaf biomass. Gunnarsson (1990) found a positive correlation between spider abundance and density of spruce needles. Similarly, Hatley and MacMahon (1980) noted that both spider numbers and density increased when they tied branches of sagebrush together, thereby increasing foliage density. Despite lower leaf biomass, the more dense or clustered arrangement of sugar maple leaves per unit of branch length, compared to white ash, may account for the greater abundance of spiders on sugar maple branches. For both web-

Table 5.—Examples of foraging-guild composition (web spinner vs hunter) reported for arboreal spiders in North American forests, orchards and plantations.

References	Tree species	Percent of individuals by guilds	Sampling method
Dahlsten et al. 1977	white fur	64% web 36% hunt	unknown
Dondale 1956	apple	62% web 38% hunt	mostly tapping branches, some hand collecting and fumigation
Halaj et al. 1996	Douglas-fir	web dominant coastal, hunt dominant inland	beating branches, lower canopy
Jennings 1976	black walnut plantation	14% web 86% hunt	hand collecting from the ground
Jennings & Diamond 1988	balsam fir spruces	slightly more web	pole pruner with catchment basket; branches lowered, cut, and bagged
Jennings & Collins 1987	red spruce	54% web 46% hunt	pole pruner with clamping device, cut and dropped onto ground cloth
Jennings et al. 1990	balsam fir, red spruce	68% web 32% hunt	pole pruner with catchment basket; branches cut, lowered and bagged
Mason 1992	Douglas-fir, true firs	hunt dominant one site, web dominant second site	beating branches
Mason et al. 1997	Douglas-fir, grand fir	47.3% web 52.7% hunt	pole pruner with catchment basket, branch beaten in plastic drum
Renault & Miller 1972	fir, spruce	web dominant	shook branch after it was cut and fell to ground
Pettersson 1996	spruce	web dominant >97%	branch cut, lowered and bagged
Uetz & Dillery 1969	maple	web dominant	lower branches examined while investigators stood on the ground

building and hunting spiders, habitat structure greatly influences spider location (Robinson 1981). Leaf density arrangement may be critically important by providing better habitats for prey, providing protection from predators, providing favorable microhabitats (Almquist 1970), and presenting more suitable structure for behavioral activities such as web or retreat building (Stevenson & Dindal 1982).

For sugar maple, spider-guild composition was similar between studies. The 20-year collection consisted of 36% web spinners and 64% hunters; the 1995 study, 35% web spinners and 65% hunters. These consistent values clearly demonstrate dominance of the hunter guild on foliage of overstory sugar maple. Our guild-composition results differ markedly from that found on coniferous foliage (Table

7), where web spinners dominate. In the 20-year study, species of *Pelegrina* were the most abundant group recovered from sugar maple. More commonly referred to as jumping spiders, salticids are noted for their large specialized anterior median eyes which give them superior eyesight compared to other spiders (Jackson & Pollard 1996). Unlike *Philodromus rufus* (dominant in the 1995 study), a hunter with relatively poor vision, salticids (including *Pelegrina proterva*) may have an advantage when ambushing prey. Previously, *P. proterva* has been found on black walnut, *Juglans nigra* L.; balsam fir, *Abies balsamea* (L.) Mill.; white pine, *Pinus strobus* L.; loblolly pine, *P. taeda* L.; shortleaf pine, *P. echinata* Mill.; common persimmon, *Diospyros virginiana* L.; peach, *Prunus persica*

Batsch (Jennings 1976); apple, *Malus* spp.; (Dondale 1956) and spruces, *Picea* spp. (Jennings & Dimond 1988).

The 20-year collection was examined prior to the 1995 study and, consequently, we predicted that *Pelegrina proterva* would be common among the more intensive samples taken at Heiberg Forest. However, this species accounted for only 0.5% of the total collection in 1995. Undoubtedly, many factors influenced spider abundance, composition and diversity in both collections. For example, in the long-term survey sugar maple branches were clipped with pole pruners and allowed to drop. Although most of these samples were caught before hitting the ground, spiders of both guilds could easily have been lost. Lost specimens may, in part, explain the similarity in total spiders collected in the two studies. Also, the 1995 collection took place throughout the growing season, whereas 1975–1995 sampling occurred during a very narrow time frame. Despite the large difference in sample sizes ($n = 40$ branches, 1-yr study; $n = 3,000$ branches (150/yr), 20-yr study), 694 individuals were obtained in 1995 (Table 1) and 712 in the 20-year collection (Table 4). Nonetheless, the 20-yr study yielded more species of spiders than the 1-yr study, as might be expected. In shrub (e.g., Hatley and MacMahon 1980), agricultural crop (Sunderland and Samu 2000) and forest (e.g., Stratton et al. 1979) communities, spider species composition can be significantly altered with changes in habitat structure. Alteration of structure affects habitat heterogeneity and microclimate, both of which play major roles in determining the composition of spider communities (Post & Reichert 1977). The northern hardwood stands that were sampled annually for two decades changed visibly in terms of canopy density and crown size over time. Typically, crowns in most northern hardwood stands tend to close with increasing stand age and a natural stratification of crowns occurs due to unequal growth rates and genetic differences (Nyland 1996). It is reasonable to assume the microclimate throughout the canopy and within individual crowns, and crown structure as a habitat for spiders, would change as well. Another factor that may have contributed to lower spider diversity in 1995 compared to the 20-year collection is that the two regions occur in different geographic provinces, even

though the study sites were only 140–180 km apart. Spider community structure and composition in forested communities vary with changes in geographic location and in different biotypes. This may occur even though the composition of these plant communities is similar, the locations where sampling occurs exist within a relatively small geographic area and locations are sampled on the same date (Renault & Miller 1972; Halaj et al. 1996). The two sample locations in the present study occur in two different broad ecological provinces; that is, climatic subzones controlled mainly by continental weather patterns (Bailey et al. 1994). At a larger scale, these locations also represent quite different forest ecosystems based on soils, topography, local weather, land use history and elevation. The site used in 1995 is located in the Northeast Appalachian Zone and the long-term study took place in the Western Adirondack and Adirondack Foothills zones (Stout 1958).

It is unlikely spiders, either singly or as a collection of species, have the type of predatory response capable of preventing outbreaks of folivores in forest or orchard ecosystems. They may play an important role, however, as regulators when pest populations are sparse (Renault & Miller 1972; Miliczky & Calkins 2002)). Knowledge of spider habits and requirements (Uetz 1991) have reached a level where it may be possible to enhance their pest control potential by maintaining or creating more suitable habitats; that is, by taking a “conservation” approach to biological control (sensu DeBach 1964). Additional work on spider diversity and ecological requirements in northern hardwood stands with differing geographic locations, dissimilar species composition and variable tree age class distributions may provide the ecological background needed to enhance the role of these predators in the natural control of certain forest pests.

For total spiders, dominant taxa and web spinners, within-crown distribution analyses indicated no significant habitat selection by spiders for either mid- or lower crown strata or for basal or distal portions of sugar maple branches. However, significantly fewer hunters were found in distal portions of mid-crown sugar maple branches. The dominant species on both overstory sugar maple and white ash overstory in the northern hardwood stands studied was *Philodromus rufus*. White ash had

fewer spiders and fewer species of spiders/100 g leaf weight compared to sugar maple. Understory foliage was dominated by *Enoplognatha ovata*, and this species was also the second most abundant spider on sugar maple overstory.

Unlike spider-guild composition of some conifers, more hunters than webspinners occurred on both sugar maple (hunters 65%, web spinners 35%) and white ash (hunters 63%, web spinners 37%) in 1995. For this intensive study, *Philodromus rufus* was the dominant hunter. The 20-year collection from sugar maple foliage in northern New York also indicated that hunters (64%) dominated, but in this sample *Pelegrina proterva* as the most common species recovered.

For future studies of arboreal spiders on broad-leafed trees, our results indicate that an intensive sampling protocol (i.e., larger sample within trees, branches cut and lowered) be employed for more than one season.

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***XYSTICUS BREVIDENTATUS* (THOMISIDAE): FURTHER RECORDS AND FIRST DESCRIPTION OF THE FEMALE**

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ABSTRACT. The male of *Xysticus brevidentatus* Wunderlich 1995 was originally described from Dubrovnik in Croatia, but females have remained unknown. During a revision of museum material in Vienna further specimens including both males and associated females from Albania, Italy and Yugoslavia were discovered. The morphology of the male pedipalp allows the placement of *X. brevidentatus* in the *cristatus* group which contains, among others, *X. cristatus* (Clerck 1757), *X. audax* (Schränk 1803), *X. macedonicus* Šilhavý 1944 and *X. pseudocristatus* Azarkina & Logunov 2001. Detailed analyses of the females showed that the shape of the female epigyne and vulva is consistent with the general scheme of the *cristatus* group and that the specimens can, due to a number of distinctive characters, be regarded as the females of *X. brevidentatus*.

Keywords: Araneae, Thomisidae, *Xysticus*, taxonomy, Balkans, *cristatus* group

The thomisid fauna of the Balkans was reviewed by Šilhavý (1944) who provided not only a species list, but also descriptions of two new *Xysticus* species, namely *X. macedonicus* Šilhavý 1944 from Macedonia and *X. tenebrosus* Šilhavý 1944 (and subspecies) from Herzegovina and Macedonia. Both species were described only from males; females remained unknown. More recently, another new species, *X. brevidentatus* Wunderlich 1995, was reported from Dubrovnik, but again the female remained unknown. In their studies of the *cristatus* group within *Xysticus* both Azarkina & Logunov (2001) and Jantscher (2001a) dealt with the problem of separating the closely related and very similar species *X. cristatus* (Clerck 1757) and *X. audax* (Schränk 1803) and both included in their analyses a third *cristatus* group species. Azarkina & Logunov (2001) mainly focused on the eastern Eurasian region and described *X. pseudocristatus* while Jantscher (2001a), who reviewed central European specimens, redescribed *X. macedonicus* including the previously unknown female.

During a revision of material lodged in the Vienna museum further *cristatus* group specimens comprising males from Castelnovo (now called Herceg Novi, Yugoslavia), Aspromonte (Calabria, Italy) and northern Albania as well as possibly associated females from northern Albania, were discovered. The males

from the latter locality, which unequivocally belong to *X. brevidentatus*, were probably collected syntopically with female *Xysticus*. These specimens may well represent the unknown *X. brevidentatus* females since they can be distinguished from all other members of the *cristatus* group. The affiliation of these female specimens to the Balkan species *X. tenebrosus* can be excluded since *X. tenebrosus* does not belong to the *cristatus* group but rather to the genus “*Psammitis*” as proposed by Jantscher (2002) and thus the predicted shape of the *X. tenebrosus* epigyne is supposed to look completely different. The present paper is a redescription of *X. brevidentatus* including a detailed study on the probable *X. brevidentatus* females and includes a discussion of possible relationships based on shared characters.

METHODS

Alcohol preserved material was loaned from Senckenberg Museum in Frankfurt (SMF; the holotype of *X. brevidentatus*) and the Naturhistorisches Museum in Vienna (NHMW; all other material). The specimens were studied using a Wild M8 binocular while an Olympus BH-2 microscope was used for higher magnification. A camera lucida attachment was used for the drawings (hairs generally omitted). All measurements are given

in millimeters. The leg spination is presented for each leg separately, starting with the number of spines on the dorsal—prolateral—ventral—retrolateral side of each segment (Fe—Mt). The spines are usually arranged in rows or double rows (ventral sides of Ti and Mt), the latter case being indicated by a “+”. Occasionally spines are less robustly developed than usual. These are marked by an additional “w” (for weak) next to the relevant number of spines.

Abbreviations.—ALE/AME = ratio of distance AME—ALE/diameter of one AME; AME = anterior median eyes; ALE = anterior lateral eyes; AME/AME = ratio of distance between AME/diameter of one AME; BL = body length; Fe = femur; LI–IV = legs I–IV; LTA = lateral tegular apophysis; Mt = metatarsus; LTA = lateral tegular apophysis; Pa = patella; PE = posterior eyes; PL = prosoma length; PME = anterior median eyes; PLE = posterior lateral eyes; PW = prosoma width; PE/AME = ratio of distance between PME—PLE/diameter of one AME; Ti = tibia.

For more information on color pattern/spination and genital structures refer to Jantscher (2001b).

REMARKS

A comparison of the genital morphology with other members of the *cristatus* group reveals that for both sexes of *X. brevidentatus* the most similar sets of characters are found in *X. macedonicus*. This species also occurs in the Balkans (e.g. Deltchev 1990) but spreads as far north as Bavaria (Muster 2000). In the present paper *X. macedonicus* is regarded as the probable sister group due to shared characters in the genital morphology.

For the males, shared characters can be found not only in the lateral tegular apophysis (LTA) but also in the shape of the embolus. The LTA is broad and expansive in both species, although there are unique features here in *X. brevidentatus*, e.g. the crest-shaped bulge (Fig. 2, c) on the lower edge, the second distinct tip or the gentle, less sclerotized structure within the curvature of the “shovel”. This less sclerotized structure is quite similar in general appearance in both *X. brevidentatus* and *X. macedonicus*. The distal part of the embolus is, in comparison with *X. cristatus* or *X. audax*, enormously enlarged, but while it is broad and short in *X. macedonicus* (e.g.

Jantscher 2001a, figs. 5, 6, 11) it is extremely long in *X. brevidentatus*. Although it must be mentioned here that the single specimen from Calabria (NHMW) is somewhat different as both the embolus and tutaculum (pocket-like sheath on the retrolateral side of the cymbium protecting the distal part of the embolus, see Fig. 2, t) are unusually short.

The similarities between *X. brevidentatus* and *X. nubilus* Simon 1875 (see e.g. Simon 1932, fig. 1213) mentioned by Wunderlich (1995) appear to be only superficial and due rather to the rotation of the axis of the median tegular apophysis towards the basal region of the bulb than to the lateral tooth. Moreover the lateral tegular apophysis of *X. nubilus* is simple in structure and the tiny tooth beneath the base of the median tegular apophysis is lacking completely in *X. nubilus*. Instead a sclerotised ridge is present.

Females show, as is typical within the *cristatus* group, a broad range of variability in their genitalia and like all *cristatus* group females (e.g. Azarkina & Logunov 2001; Jantscher 2001a) are difficult to separate from each other. The main reason for this variability is obviously the membranous structure of the genital duct, which is in the proximal part enormously widened (sack-like structure) and then towards the receptacula contracts again and forms distinct bulges and twists. For this reason the angle at which the vulva is examined plays a crucial role in accurate identification. The vulva must be placed evenly and not viewed at a different angle. The broad range of epigynal/vulvar variation becomes obvious in comparison of Figs. 6–17.

However, with regard to other *cristatus* group females, we find the greatest character correlation between females of *X. brevidentatus* and *X. macedonicus*. The epigynes of both species are very similar and are barely separable, which is reminiscent of the problem with the epigynes of *X. cristatus* and *X. audax* (e.g. Azarkina & Logunov 2001; Jantscher 2001a). A specific character shared between them is the presence of elongate lateral plates (Fig. 6, sp) on each side of the median septum (Fig. 6, ms). But again, the vulvar structure of *X. brevidentatus* and *X. macedonicus* is different. Here special attention must be paid to the duct region which connects the receptacula and the membranous part of the base of the grooves. This region is characteristically

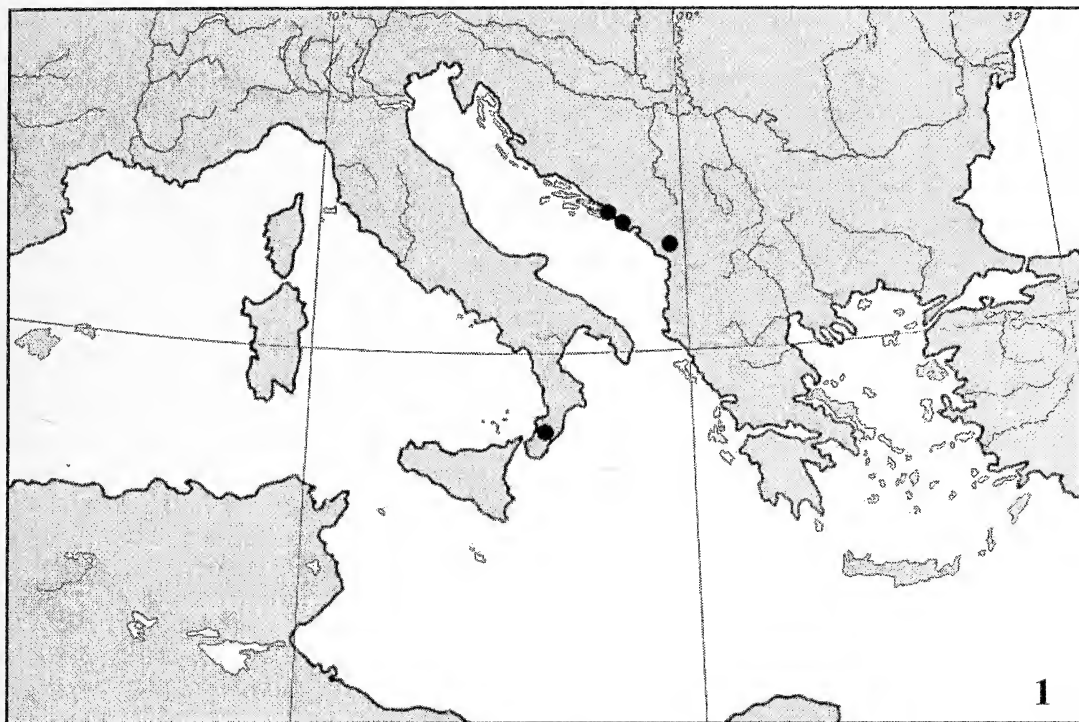


Figure 1.—Known distribution of *Xysticus brevidentatus*.

twisted in *X. brevidentatus* but takes a more simple and more gentle course in *X. macedonicus*. Again *X. nubilus* females (see e.g. Simon 1932, fig. 1236) differ strikingly from the shape of the *X. brevidentatus* epigyne. The broad range of intraspecific variation of the genital morphology is comparable to that observed in *X. cristatus* or *X. audax* (e.g. Jantscher 2001a) and is demonstrated in Figs. 6–17.

Xysticus brevidentatus was only known from the type locality in Croatia and, based on the NHMW material, is now also reported from northern Albania, Yugoslavia and Italy. Unfortunately we lack any information on its ecological requirements as there are no hints on the museum labels nor in the original description. More material and data are desirable for an insight into the ecology and zoogeography of this species.

Xysticus C.L. Koch 1835
“*cristatus* group”

Xysticus brevidentatus Wunderlich 1995
(Figs. 1–17)

Xysticus brevidentatus Wunderlich, 1995:754, figs. 20–22.

Type.—Holotype male, Dubrovnik, Former Yugoslavia (now Croatia) (SMF 5546).

Other material examined.—2 ♂, 8 ♀, northern Albania, Penther leg. (NHMW); 1 epigyne [without body], Castelnovo [now Herceg Novi; Montenegro, Yugoslavia] (NHMW); 1 ♂, Italy, Aspromonte, (Calabr.), Paganetti-Humler, 1906 (NHMW).

Diagnosis.—*Xysticus brevidentatus* can be separated from similar species of the *cristatus* group by the highly specific and complex structure of the lateral tegular apophysis, which not only bears a distinct, crest-like bulge (Fig. 2, c) on its prolateral edge but also shows a second strongly sclerotized, marginally serrated extension. In comparison to other *cristatus* group species the embolus is distinctly enlarged and massive.

The general appearance of the female epigyne is nearly identical to *X. macedonicus* (e.g. Jantscher 2001a, figs. 19, 20, 21). It also shows elongate side plates (Fig. 6, sp) beneath the median septum (Fig. 6, ms) but can be separated from *X. macedonicus* by the vulvar structure. Before reaching the receptacula, the genital duct (planar, dorsal view), is twisted in

X. brevidentatus but takes a more straight course first and then gently turns around towards the receptaculum in *X. macedonicus*.

Description.—*Male*: measurements ($n = 3$): BL: 4.0–4.7; PL: 2.1–2.4; PW: 2.1–2.3; AME/AME: 4.7–5.1; PE/AME: 5.2–5.3; ALE/AME: 2.6–3.1.

Color and structure: Prosoma dorsally dark to middle brown with a distinct white marking, more or less forming a “U” shape (rein-shaped marking—see Jantscher 2001b). It is anteriorly rather narrow but reaches the yellow-cream colored eye-field. The median field, i.e. the area enclosed by the U-shape is middle brown and medially divided by a white, longitudinal line. The anterior eyes and PLE are embedded in a light, white stripe. The lateral areas of the tergum are dark middle brown and show only a slight pattern. Clypeus frontally set with 7 spines. Clypeal margin centrally somewhat elongated to form a small, triangular prong between the chelicerae. The transition tergum/clypeus is angular and steep. Chelicerae frontally set with spines, distally and proximally brown, in between cream colored. Sternum elongate-oval with a yellow-brown margin around a cream colored area. Opisthosoma dorsally with a white margin enclosing an oval light-brown field with a white folium (zigzag shaped pattern). Ventral side beige to cream colored.

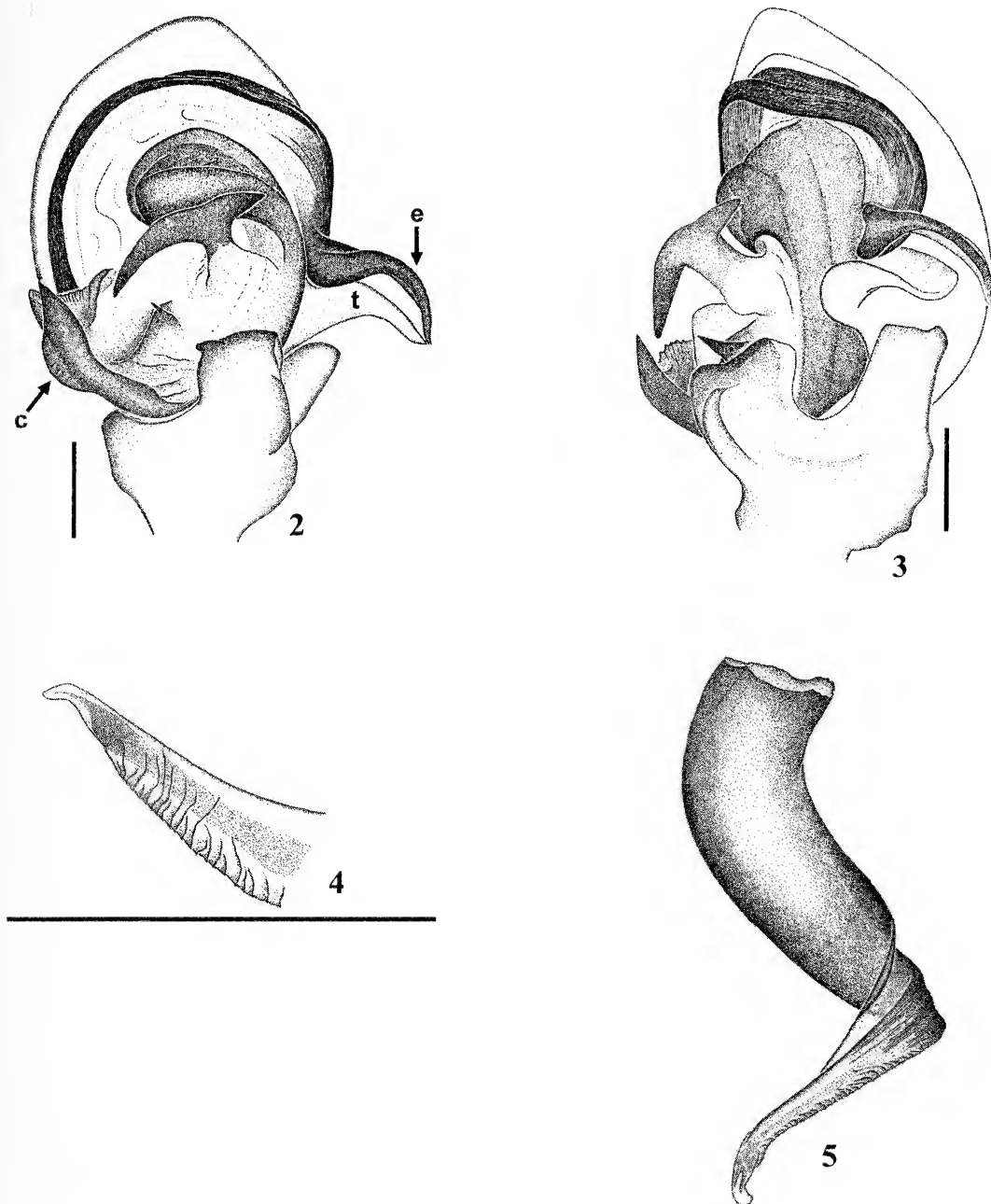
Legs and spination: Middle brown, proximally yellow-brown. A cream colored median stripe is present on the ventral and dorsal side but can in part be broken up on the femora. Tarsal claws with 6 teeth. Retrolateral sides of all femora with a smooth, spineless and elongate field. Spination: LI: Fe 5-18-0-0, Pa 0-1-1-1, Ti 0-3-4+4-3, Mt 0-3-3+2-3, LII: Fe 8-0-0-0, Pa 0-1-1-1, Ti 0-3-4+4-3, Mt 0-3-4+3-3, LIII: Fe 4-0-0-0, Pa 1-1-0-1, Ti 1-2-3+3-2, Mt 0-3-2+2-3, LIV: Fe 5-0-0-1, Pa 1w-1-0-1, Ti 2w-2-3+3-2, Mt 0-3-2+2-3.

Pedipalp (Figs. 2–4): Tibia with two apophyses. Ventral apophysis in ventral view more or less rectangular with a slanting distal edge. Additionally a tiny projection on the prolateral distal edge is present. Retrolateral tibial apophysis in ventral view massive and club shaped, tapering off towards the tip, in retrolateral view also more or less rectangular (Fig. 3). The complex structured tegulum bears a T or hammer-shaped median tegular apophysis and a broad lateral apophysis. Both

ends of the median apophysis are pointed, with the prolateral branch being distinctly longer than the retrolateral branch. The horizontal angle is slightly turned downwards, i.e. the tip of the median tegular apophysis points towards the tibia. The whole area of the lateral tegular apophysis is shovel-shaped and forms in ventral view two distinct tips. The uppermost (i.e. most ventral) tip is formed by the strongly sclerotized margin of the shovel and is distally blade-like and pointed. On its prolateral edge a distinct crest-shaped bulge (Fig. 2, c) is visible. The, in ventral view, triangular area behind this tip is marginally serrated and forms the second tip. The retrolateral view (Fig. 3) reveals the presence of two further structures. A thin and rather large but only slightly sclerotized, blunt structure is present as well as a distinct thin, but very sharply pointed tooth. Both structures are easily overlooked in ventral view, but are rather distinct in retrolateral view. The blunt structure is represented by an inconspicuous ridge in ventral view. The strap-like embolus (Fig. 2, e) encloses the bulb in a half-circle. Its last third is slightly twisted to make a lateral-turn to the retrolateral side. The distal part of the embolus is conspicuously large and massive (Figs. 2, 4). The tutaculum (Fig. 2, t) beneath it is also very large and points to the retrolateral side. Higher magnification reveals that the surface of the embolus is not completely smooth but exhibits fine folds and scales (Fig. 5)

Description.—*Female*: Measurements ($n = 7$): BL: 6.3–7.4; PL: 2.6–3.1; PW: 2.6–2.9; AME/AME: 5.4–6.9; PE/AME: 4.9–6.9; ALE/AME: 2.9–3.6.

Color and structure: Prosoma dorsally dark brown to middle brown with a distinct white marking which more or less forms a “U” shape. The median field, i.e. the area enclosed by the U-shape, is middle brown and usually divided by a light, longitudinal median line. U-shaped markings cream colored and anteriorly reaching the yellow-brown to cream colored eye-field. The anterior eyes and PLE are embedded in a white or cream colored stripe. Posterior to the U-shaped markings a light colored, white, cream or pale white rectangular field is present. On each of its sides an independent additional light patch can be present or an anchor-shaped pattern can be developed instead. Clypeus, especially medially, light colored and frontally set with 7 spines.

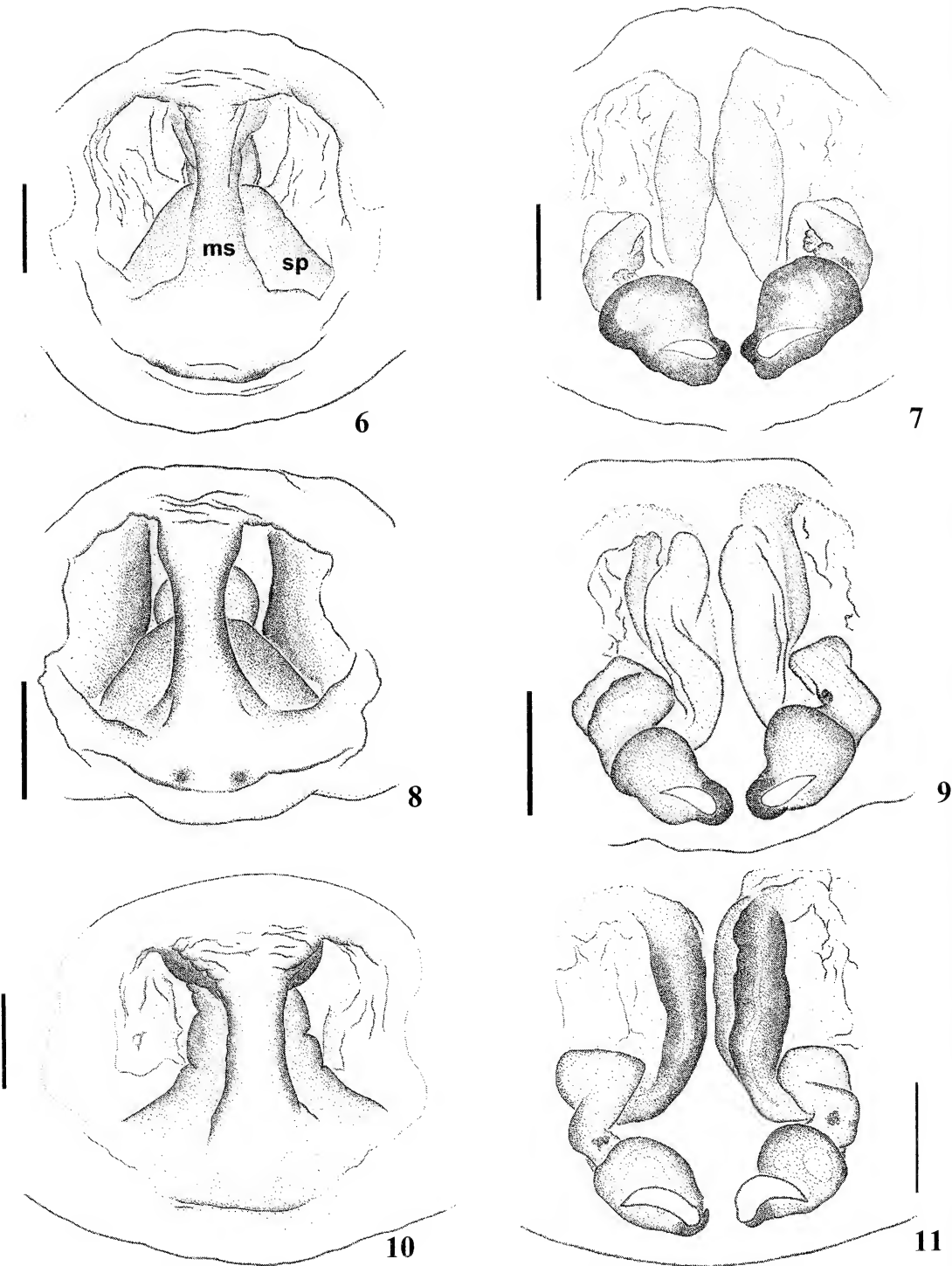


Figures 2–5.—*Xysticus brevidentatus*, specimen from northern Albania: 2, 3, Left male pedipalp: 2. Ventral aspect; c = crest on LTA, e = embolus, t = tutaculum; 3. Retrolateral aspect; 4, 5, Right embolus; 4. Distal region, ventral aspect; 5. Terminal region, lateral aspect. Scale = 200 μm.

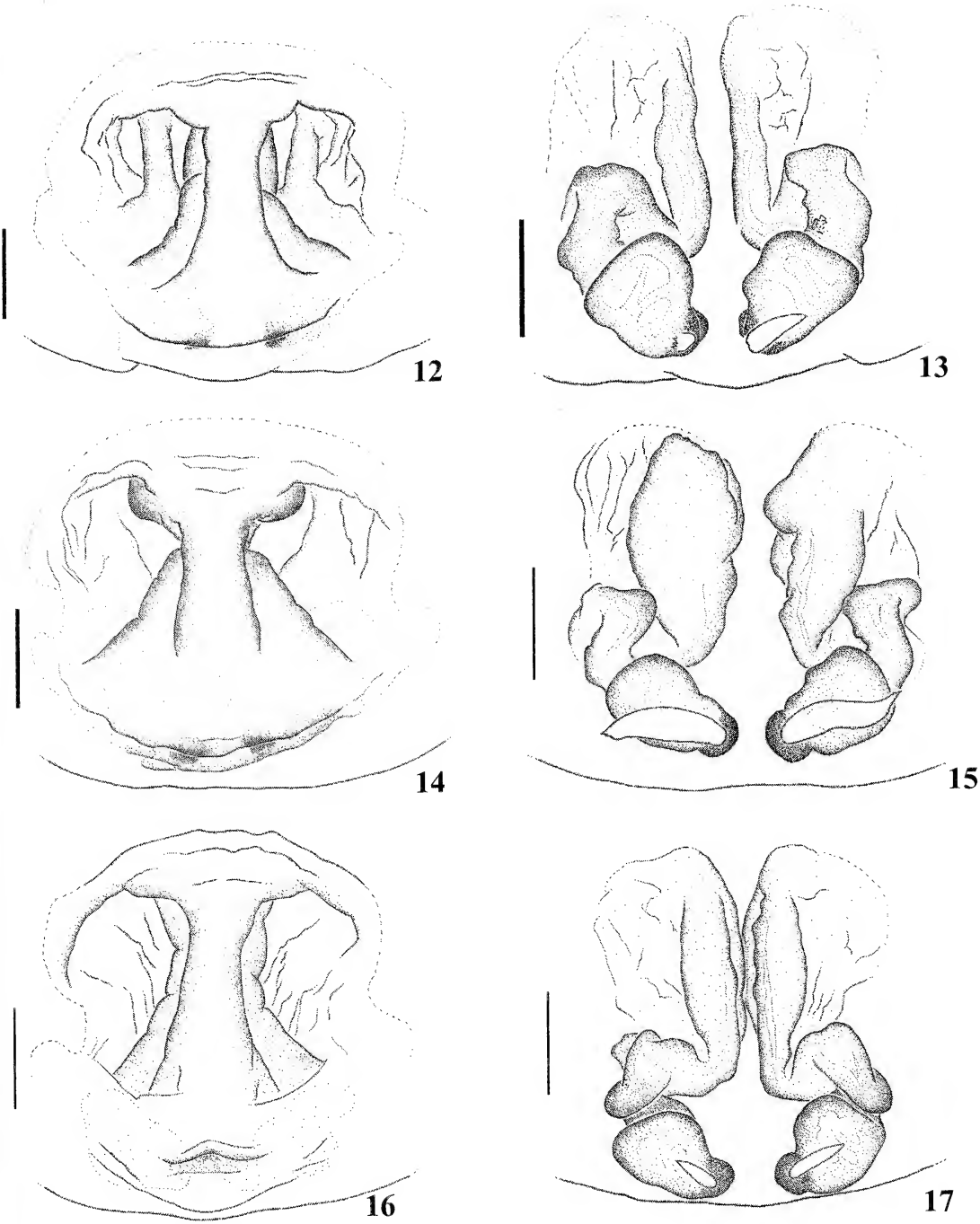
Clypeal margin centrally somewhat elongated to form a small, triangular prong medially between the chelicerae. The transition tergum/clypeus is angular and steep. Chelicerae proximally brown, distally light brown to cream colored and frontally set with spines. Sternum

elongate oval with a yellow margin enclosing a cream and brown mottled area.

Opisthosomal margin white, dorsally enclosing a gray, gray-brown or hazel brown oval area with a white folium (usually a broad lancet-shaped pattern with three transverse



Figures 6–11.—*Xysticus brevidentatus*, epigynes: 6, 7. specimen from Castelnovo. 6, Ventral aspect, ms = median septum, sp = side plate; 7. Dorsal aspect (vulva); 8–11. Specimens from northern Albania; 8, 10. Ventral aspect; 9, 11. Dorsal aspect (vulva). Scale = 200 μ m.



Figures 12–17.—*Xysticus brevidentatus*, epigyne, specimen from northern Albania: 12, 14, 16. Ventral aspect; 13, 15, 17. Dorsal aspect (vulva). Scale = 200 μ m.

stripes). Opisthosoma ventrally cream-beige to beige-brown with light brown to middle brown spinnerets.

Legs and spination: Legs robust, light-brown to middle or dark brown, legs I and II

can either be distally somewhat darker or are generally considerable darker. Prolateral sides of femora often light colored with cream and brown dots and/or brown rings around the spinal bases. Cream or yellow-cream colored me-

dian stripes are present on the ventral and dorsal side (coxa to tarsus) but can in part be broken up on the femora. Tarsal claws with 4–5 teeth. Coxae ventrally brown with inconspicuous white pattern. Retrolateral sides of all femora with a smooth, spineless and elongate field. Spination: LI: Fe 0-3-0-0, Pa 0-0-0-0, Ti 0-0-3+4-0, Mt 0-3-4+4-3, LII: Fe 1-0-0-0, Pa 0-0-0-0, Ti 0-0-4+4-0, Mt 0-3-4+4-3, LIII: Fe 1-0-0-0, Pa 1w-0-0-0, Ti 1w-2-3+2-0, Mt 0-3-2+2-3, LIV: Fe 1-0-0-0, Pa 1w-0-0-1w, Ti 2-2-3+0-0, Mt 0-3-2+2-3.

Epigyne (Figs. 6–17): Epigyne shows a median septum which separates two epigynal grooves. The usually slender, but not especially narrow, septum is accompanied on each side by side plates. These structures are enormously variable both in shape and degree of sclerotization (Figs. 6, 8, 10, 12, 14, 16). Usually one plate consists of several often bulgy components. The posterior region of the groove is dominated by one distinct segment which broadens posteriorly. The lateral margins of the grooves are characterized by several folds and edges. Occasionally the base of the grooves are distinctly marked with sclerotised folds, giving the impression of column-shaped structures. The posterior margin of the grooves is situated some distance away from the epigastric fold. The vulvar structure (Figs. 7, 9, 11, 13, 15, 17) is rather complex and consists of a huge, membranous area, a distinct duct and the receptacula. The membranous area is formed by the soft and dilatable bases of the grooves which contract medially to form the duct-section. Here there is not a simple horizontal passage but instead a twisted course, leading to the receptacula which show an inner compartmentalization. Translucent fertilization ducts are attached to the receptacula at their medial margin. Glands are present anterior to the receptacula within the folds of the duct.

Distribution.—This species has been found in Croatia, northern Albania, Yugoslavia and southern Italy (Fig. 1).

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THE FIRST FOSSIL CYPHOPHTHALMID (ARACHNIDA, OPILIONES) FROM BITTERFELD AMBER, GERMANY

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ABSTRACT. The first fossil cyphophthalmid harvestman, *Siro platypedibus* new species (Arachnida, Opiliones, Cyphophthalmi), is described from Bitterfeld amber, Sachsen-Anhalt, Germany. The age of this amber is in dispute. Geological studies support a Miocene (20–22 Ma) date for the deposit, but the presence of insect species identical to those in Baltic amber (dated at ca. 35–40 Ma) has led other authors to suggest that the Bitterfeld amber comprises older, redeposited material, contemporary with Baltic inclusions. Two features in this harvestman fossil are consistent with the Recent genera *Siro*, *Paramiopsalis* and *Tranteeva*: (a) smooth tarsi and metatarsi in legs 1 and 2 and (b) the apparent absence of a dorsal crest on the basal article of the chelicera. Unequivocal autapomorphies of any one of these genera are not clearly preserved in this fossil, but *Paramiopsalis* is a monotypic Iberian genus, and *Tranteeva* is a monotypic genus from Bulgaria, while *Siro* is more diverse and widely distributed, including living representatives in Central Europe relatively close to the Bitterfeld type locality. For this reason we assign the fossil to *Siro*.

Keywords: Cyphophthalmi, Sironidae, *Siro*, taxonomy, paleontology, new species

Fossil harvestmen are rare and their fossil record is currently restricted to a few Paleozoic and Mesozoic examples together with a more diverse Tertiary record based principally on the Florissant Formation and on Baltic and Dominican ambers; see e.g., Petrunkevitch (1955), Cokendolpher & Cokendolpher (1982) and Selden (1993) for reviews. The majority of the fossil harvestmen have been referred to, or strongly resemble members of, the Eupnoi and Dyspnoi clades. Among those specimens which have not been formally described there is a very old (c. 340 Ma), but remarkably modern-looking, phalangiid harvestman (Wood et al. 1985), which implies for this group a high degree of morphological conservatism over geological time. Laniatores is currently known only from Tertiary ambers, and all of the Dominican amber harvestmen described thus far are Laniatores (Cokendolpher & Poinar 1998). The remaining suborder, Cyphophthalmi, has not previously been recorded in the fossil record. Petrunkevitch (1949) claimed that some of the Pennsylvanian Coal Measures harvestmen distinctly resembled cyphophthalmids, but his arguments

are unconvincing. These Coal Measures fossils lack autapomorphies of Cyphophthalmi and are relatively large with long, slender legs in at least some specimens.

Cyphophthalmi are small to medium-sized, inconspicuous, almost mite-like, creatures with short, stubby legs which typically live in soil, leaf litter or caves (Shear 1980). They are often regarded as primitive harvestmen and recent phylogenetic studies (Shultz 1998; Giribet et al. 1999, 2002) have consistently placed them in a basal position, as sister-group to the remaining opilionids. The fossil record provides minimum divergence times for clades, thus the recently published cladograms predict that the cyphophthalmid lineage should go back to at least the mid-Paleozoic, the age of the oldest recorded harvestman (see above). The systematics of the Recent cyphophthalmids have been summarized by the catalogue of Giribet (2000), who recognized 113 extant species in 26 genera, and the cladistic analysis of generic relationships by Giribet & Boyer (2002). We refer to these publications for additional background literature on the group. In this paper we describe the first fossil

cyphophthalmid, a specimen discovered in the Berlin collection of inclusions from the Bitterfeld amber deposit of eastern Germany.

METHODS

The holotype, and only specimen, was informally recognized as a cyphophthalmid in 1989 by Manfred Moritz, the then Curator of Arachnids in the Zoology Department of the Museum für Naturkunde, Berlin. It was thus discovered too late to be listed in the summary paper of Schumann & Wendt (1989) on Bitterfeld inclusions. The fossil was not subsequently formally described. The specimen is held in the Arthropod Section of the Paleontology Department of the Museum für Naturkunde Berlin (MB.A.) under the repository number 1086. Drawings were prepared with the aid of a camera lucida attachment and the fossil was compared to all extant genera of Cyphophthalmi and to most species of Sironidae (see e.g. Giribet & Boyer 2002, Appendix 2). Digital photographs (Figs. 1–2) were taken using a JVC Digital Camera KY-F70B mounted on a Leica MZ 12.5 stereomicroscope. Series of ca. 20 images were taken at different focal planes and assembled with the dedicated software package Auto-Montage 4.01.0085 by Synoptics Ltd. All measurements are in mm.

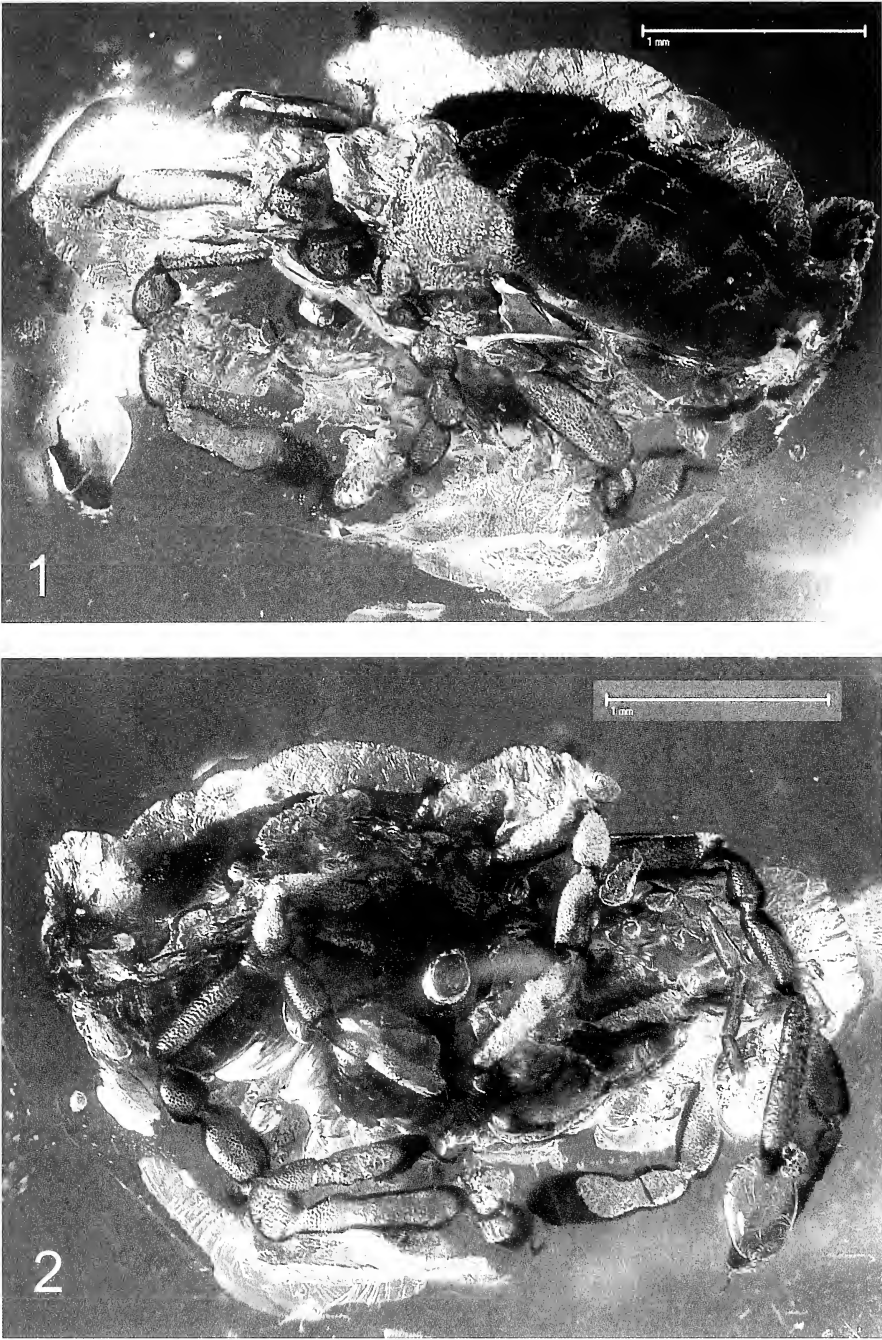
BITTERFELD AMBER

Amber from the Bitterfeld region of Germany has been known since at least the mid 17th century; see Kosmowska-Ceranowicz & Krumbiegel (1989) for a review. This Bitterfeld, or Saxon (=Saxonian), amber is not as well known as Baltic or Dominican amber. The locality was originally kept secret by the German Democratic Republic on the suspicion that it was associated with uranium deposits (M. Barthel, pers. comm., 2003), but in recent years it has seen increased activity from amateur collectors. It nevertheless contains a diverse range of inclusions, provisionally listed by Schumann & Wendt (1989). Although there have been numerous papers on the plants, fungi and, especially, the insect fauna (e.g. Röschmann 1997; Wagner et al. 2000), the arachnids remain quite poorly studied with only a few formal species descriptions (e.g. Wunderlich 1993). The first concerted study of the inclusions was by Barthel & Hetzer (1982). These authors figured a number of

taxa, including some spiders and a well-preserved phalangiid harvestman, and provided an overview of the geological setting. Further geological details can be found in Führmann & Borsdorf (1986) and Kosmowska-Ceranowicz & Krumbiegel (1989).

Geological setting.—Historically, amber has been recovered from a number of sites in the vicinity of Bitterfeld and the adjacent Mulde river in the Sachsen-Anhalt region of eastern Germany (see e.g. Kosmowska-Ceranowicz & Krumbiegel 1989, fig. 1). Since 1955 the principal source of amber, almost certainly including the specimen described here, has been the now disused, open-cast Braunkohl mine of Goitsche near Bitterfeld. The amber-producing horizon consists of a series of massive, sandy-clay lenses which, according to the local geological terminology, lie between the Bitterfeld main coal seam and the Breitenfeld seam (Kosmowska-Ceranowicz & Krumbiegel 1989, fig. 3). The sand and clay have been interpreted as representing a period of marine ingressions which was dated on spore evidence to sporomorph zone IIIA according to the German Democratic Republic stratigraphic scale for the Tertiary (Krutsch in Barthel & Hetzer 1982). This spore zone correlates to a lower Miocene (lower Aquitanian) age.

Age of the amber.—Amber is notoriously difficult to date precisely and the Bitterfeld inclusions have been assigned to anything between an Eocene and a Miocene age. Barthel & Hetzer (1982) interpreted Bitterfeld amber as younger than Baltic amber, dating the former at lower Miocene (ca. 22 Ma) based on a combination of the regional geology and microbotany (see above). The inclusion-bearing pieces unequivocally lie in situ in strata associated with the Miocene coal seams (M. Barthel, pers. comm., 2003). Wunderlich (1983) suggested that the Bitterfeld amber was merely part of the Baltic amber complex and thus implicitly late Oligocene/Eocene (ca. 35–40 Ma) in age. He derived these conclusions from a (very provisional) survey of similar faunal (spider) and floral elements in both ambers. Führmann & Borsdorf (1986) supported the Miocene age and rejected this redeposition hypothesis. These authors presented a detailed physico-chemical analysis in which they argued that the composition of mineralogical species in Bitterfeld amber dif-



Figures 1–2.—*Siro platypedibus* new species; the first fossil cyphophthalmid. MB.A. 1086 from Bitterfeld amber, Sachsen-Anhalt, Germany. 1. Dorso-lateral aspect; 2. Ventro-lateral aspect. Scale bars = 1 mm.

ferred significantly from that of Baltic amber. Kosmowska-Ceranowicz & Krumbiegel (1989) analyzed the heavy mineral composition in the amber-bearing sediments and compared them to strata of known age in the same

region. Their main conclusion was that an Eocene age for the amber-bearing sediments could be ruled out, but that the sediments could represent redeposited Oligocene material. Note that these results apply to the sedi-

ments and not the amber itself. These authors also noted a degree of color variation in the Bitterfeld amber which is not seen in Baltic amber, again implying that these ambers come from different sources.

However, Röschmann (1997, and references therein) has challenged the assumption that the Baltic and Bitterfeld ambers are fundamentally different, based on a detailed comparison of insect faunas; particularly Diptera. In this study, 14 species of fossil Sciaridae were found to be common to both ambers and, in general, the Baltic and Bitterfeld fly faunas score similarly on various ecofaunistic indices. The longevity of arthropod species has been estimated at 2.5–7 million years, thus if there really is an age difference of at least 13 million years between the Baltic and Bitterfeld ambers then, assuming these longevity estimates are accurate and widely applicable, we would not expect to find identical species in them. Röschmann thus implied an older age and redeposition of the Bitterfeld material and suggested that the Baltic and Bitterfeld amber-producing forests were of a rather similar age; unlike the host sediments of the amber pieces.

It should be added that Wagner et al. (2000) gave an Eocene (50 Ma) date for both Bitterfeld and Baltic amber, but the two papers they cite in support of this (Noonan 1986, 1988) are essentially biogeographical studies, one of which mentions a date for Baltic amber of 30 Ma and neither of which mention the Bitterfeld deposit! This illustrates the danger of poorly-justified dates becoming perpetuated in the literature. It is beyond the scope of the present paper to resolve the problems of dating the Bitterfeld fossils. Rikkinen & Poinar (2000) used the younger, Miocene age of around 20–22 Ma, but Poinar (pers. comm., 2002) now accepts the idea that Bitterfeld amber could be equivalent to Baltic amber, but perhaps originating from a different geographical source to the Baltic amber forest. Our fossil can thus be constrained to, at best, an age of between 20–40 Ma.

MORPHOLOGICAL INTERPRETATION

The fossil is preserved in an oval piece of relatively clear and translucent amber. Its orientation makes it primarily visible from both sides in a dorso-lateral and ventro-lateral view respectively, thus details of the legs are easier to see than those of the body (Figs. 1–4). Un-

fortunately there is a series of internal fractures in the matrix around the body, which, along with numerous bubbles, obscures some details. There also appears to be some sort of foreign body (a spore?) directly underneath the animal which partly covers the coxo-sternal region and ventral surface of the opisthosoma. Grinding the amber would not clearly reveal the entire ventral surface without damaging the legs. Some parts of the legs are encrusted with a refractant substance, but the underlying morphology is still visible. The fossil is undoubtedly a cyphophthalmid and, like modern examples, it has a small, compact and densely tuberculate body (Murphree 1988), short, stubby legs with somewhat swollen and rounded podomeres, and a tarsus which ends in a single claw. The animal is complete and the body is c. 2 mm long, which is within the range of modern species. There is no projecting adenostyle on the fourth tarsus; therefore, since the specimen looks mature due to the degree of sclerotization, we interpret it as a female.

The carapace is mostly hidden in the matrix. There is no evidence for the presence of eyes. Ozopores on a pair of raised tubercles are characteristic for cyphophthalmids (Giribet et al. 2002) and one of these paired, raised, horn-like structures, sometimes termed ozophores, can be seen on one side of the fossil (Figs. 2, 4). It is deep within the matrix and details of morphology are lacking. Its apparently dorso-lateral position is consistent with the 'type 2' orientation (cf. Jubber 1970; Giribet & Boyer 2002). On the other side (Figs. 1, 3) the ozophore region is obscured, almost as if a secretion from it has formed an ill-defined bubble in the matrix over the antero-lateral corner of the carapace. The opisthosoma expresses at least seven tergites dorsally, each densely tuberculate with circular tubercles and separated from adjacent tergites by a narrow band of non-tuberculate cuticle.

The chelicerae are mostly obscured behind other limbs, but the dorsal surface of the basal article can be seen. Proximally, there is no evidence for a dorsal crest (= dorsal ridge) which is characteristic of many living cyphophthalmids (e.g. Giribet & Boyer 2002, Figs. 1–3). Characters relating to the ventral surface of the second article or the movable finger of the chela are equivocal. The pedipalps are

slender with elongate podomeres which are distally densely setose. The legs are robust and tend to converge distally beneath the animal. Like the body, the legs are densely tuberculate. The leg tuberculation tends to be formed from more elongate, oval tubercles, especially on the dorsal surface of the articles in legs 3 and 4. Significantly, this tuberculation is not apparent on the metatarsus and tarsus of legs 1 and 2 (Figs. 1–4). The leg formula is, from longest to shortest: 1 2 4 3. The patellae and tibiae of leg 4 are notably swollen and ovate in appearance. The legs preserve a number of setae, which become more numerous on the more distal articles. There is a particular concentration of setae on the ventral surface of the distal tarsus near the origin of the claw, but not forming a distinct solea. All legs end in a single, smooth, hook-shaped tarsal claw.

SYSTEMATIC PALEONTOLOGY

Suborder Cyphophthalmi Simon 1879

Family Sironidae Simon 1879

Genus *Siro* Latreille 1796

Siro platypedibus new species

Figs. 1–4

Type and only material.—MB.A. 1086. Holotype and only known specimen. Bitterfeld amber. From the site of the Goitsche (or Goitzsche) Mine, near Bitterfeld, Sachsen-Anhalt, Germany (c. 51°36'N, 12°22'E). Tertiary (?Oligocene–Miocene) in age. Specimen also bears the identification number “Ser. 15/4”.

Etymology.—From the tall, flattened patella and tibia in leg 4.

Diagnosis.—Ornamentation of legs as in the genera *Siro*, *Paramiopsalis* and *Tranteeva* with all tarsi and metatarsi 1 and 2 lacking the normal pattern of granulation seen in the other podomeres. Articles of legs compressed laterally with patella and tibia 4 becoming enlarged and flattened. Claws large. The appendages of this specimen are of particular interest and may indicate some special type of habitat.

Description.—Complete female cyphophthalmid. Total body length c. 2, but anterior obscured in matrix. Body with tuberculate ornament, darker than legs with at least seven clearly defined opisthosomal tergites. Prosoma with anterolateral ozophore. Chelicerae mostly obscured, but basal article 0.65 long. Pedipalps slender, podomere lengths: patella 0.33,

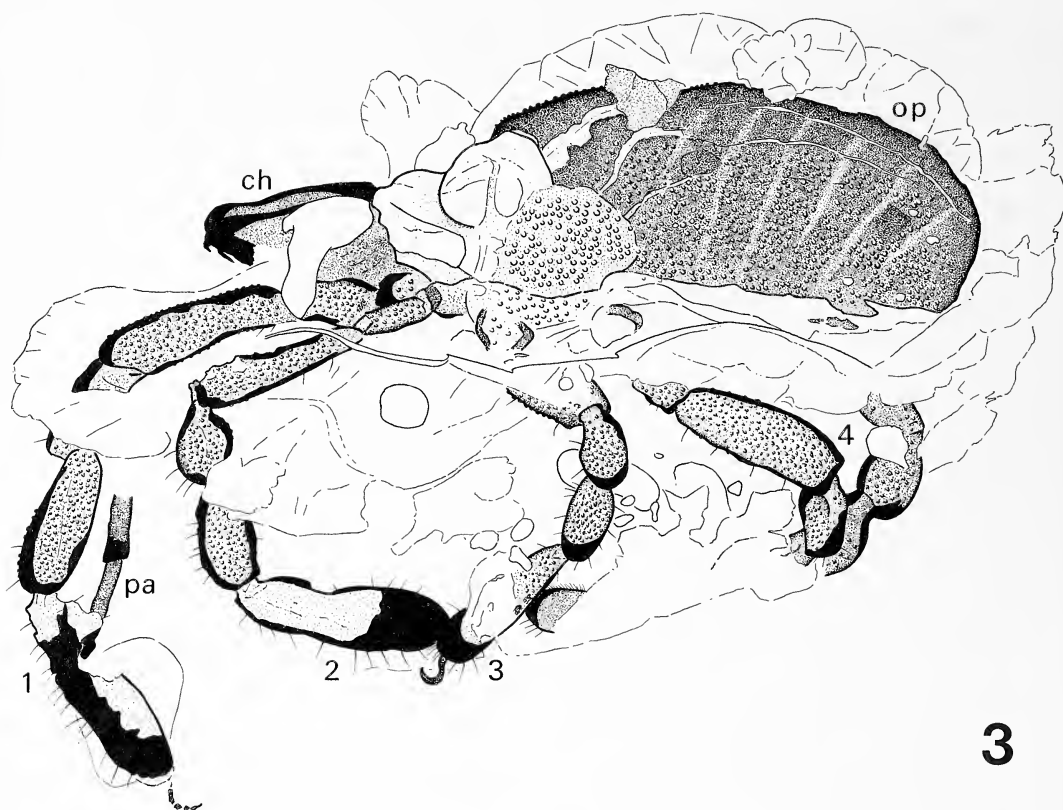
tibia 0.29, tarsus 0.27. Leg article lengths as follows. Leg 1: femur 0.75, patella 0.32, tibia 0.56, metatarsus 0.30, tarsus 0.55; total length c. 2.5. Leg 2: femur 0.65, patella 0.32, tibia 0.41, metatarsus 0.29, tarsus 0.50; total length c. 2.2. Leg 3: femur 0.45, patella 0.33, tibia 0.33, metatarsus 0.30, tarsus 0.47; total length c. 1.9. Leg 4: femur 0.58, patella 0.30, tibia 0.38, metatarsus 0.26, tarsus 0.53; total length c. 2.1. Legs tuberculate like body, but tuberculation absent on distal articles of legs 1 and 2. All legs end in single, smooth, hook-shaped claw, c. one-third the length of the tarsus.

Remarks.—This specimen represents the first, and so far only, fossil record of Cyphophthalmi. Their rarity as fossils is undoubtedly due to a combination of their unmineralized cuticle, small size and cryptic, soil-living habits; all of which reduce their chances of preservation. Amber nevertheless has the potential to trap soil or leaf-litter organisms. Schumann & Wendt's (1989) faunal list for Bitterfeld amber includes various elements of the soil meso- and macrofauna such as nematodes, isopods, oribatid mites, collembollans and myriapods.

Although there has been some northward drift of continental Europe by a few degrees over the last 40 million years, our fossil still probably represents the most northerly record of European Sironidae, c. 51–52° N. The most northerly distributed extant species in Europe is *Siro carpaticus* Rafalski 1956 which occurs in the Carpathian mountains of south-eastern Poland (c. 40°08'N). The amber fossil suggests that *Siro* was at one stage more widespread in Europe and previously occurred further north than its present geographical range. Two other sironid species occur at high latitudes in North America, *S. acaroides* (Ewing 1923) in Washington, up to 47°50'N, and *S. kamiakensis* (Newell 1943) in Washington and Idaho, c. 47°50'N.

AFFINITIES

The specimen described here lacks ventral teeth on the claw of leg 2, a character which excludes placement in the following genera: *Neogovea* Hinton 1938, *Huitaca* Shear 1979, *Metagovea* Rosas Costa 1950, *Paragovia* Hansen 1921, *Troglosiro* Juberthie 1979 and *Metasiro* Juberthie 1961 (see Giribet & Boyer 2002). Two preserved features (Figs. 1–4) are of particular interest: (a) the absence of tubercular ornament on the metatarsus and tar-



Figures 3–4.—Interpretive drawings of the specimens shown in Figs. 1, 2. Abbreviations: ch = chelicera, cx = coxae, in = unidentified inclusion beneath the animal, op = opisthosoma, oz = ozophore, pa = pedipalp, pt = patella, ti = tibia. Legs numbered from 1 to 4. Note the lack of tuberculation at the distal ends of legs 1 and 2 and the shape of the patella and tibia on leg 4. Scale bar = 0.5 mm.

sus of legs 1 and 2 and (b) the apparent absence of a dorsal crest on the basal article of the chelicera. Both of these characters are consistent with the extant genera *Siro*, *Paramiopsalis* Juberthie 1962 and *Tranteeva* Kratchovil 1958 (see e.g. Juberthie 1970, 1991; Giribet & Boyer 2002) all of which belong to the Laurasian family Sironidae. The distinct lack of ornamentation on metatarsi 1 and 2 is also found in the Japanese genus *Suzukielus* Juberthie 1970, but it has a dorsal crest on the basal article of the chelicera. The type 2 position of the ozophore is also consistent with these taxa, although this character is seen in other genera too. However, it indicates that the fossil does not belong to the sironid genera *Parasiro* Hansen & Sørensen 1904 or *Odonotosiro* Juberthie 1961, which have type 1 ozophores inserted in the margin of the carapace. Resolving the position of the fossil be-

tween the genera *Siro*, *Paramiopsalis* and *Tranteeva* is difficult based on the preserved morphology. They are differentiated from each other on characters relating to the corona analis at the posterior end of the opisthosoma, fusion of the coxae of legs 2 and 3 (in *Paramiopsalis*), the shape of the palpal trochanter, the length of the appendages, and the type of adenostyle. All these characters are either absent or equivocally preserved in the fossil and further preparation by grinding the amber is unlikely to reveal them. The appendages of *S. platypedibus* are of particular interest because they have long claws as in some of the troglolobiotic species of *Siro* and *Tranteeva*, but the legs in the fossil, instead of being elongated, are compressed laterally. This is reminiscent in a certain way of the appendages of the equatorial African genus *Ogovea* Roewer 1923 which may show fossorial behavior.

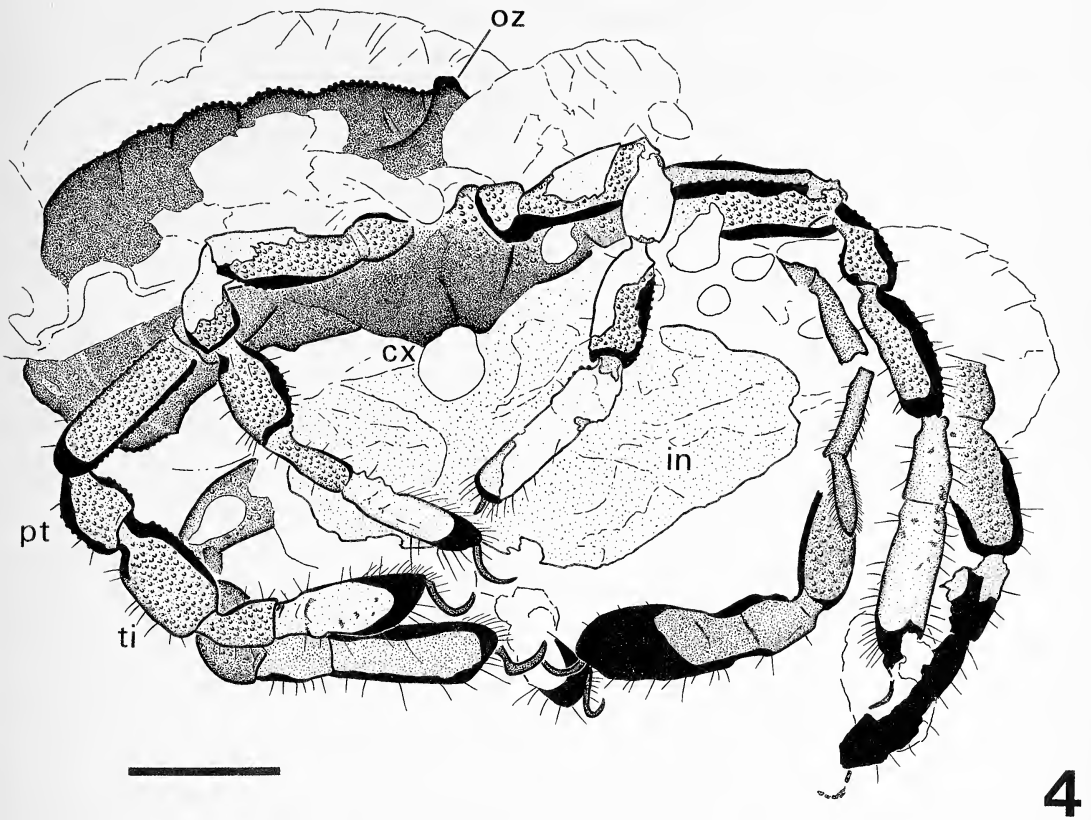


Figure 4.—Same as Fig. 3.

Paramiopsalis is a monotypic genus, currently restricted to the north-west Iberian Peninsula (Juberthie 1962; Giribet 2000). *Tranteeva* is also monotypic and restricted to some caves in Bulgaria (Kratochvíl 1958; Juberthie 1991), although there are doubts about the validity of the genus, which seems to be an apomorphic form of the Balkan sironid clade (Juberthie 1991). By contrast, *Siro* is more diverse and widely distributed, containing 23 extant species spread across Europe, Turkey and the USA. These records include Central European taxa (Austria, Slovakia, Poland) whose, albeit often localized, distribution is relatively consistent with the type locality of the Bitterfeld amber in eastern Germany. We see no characters in the fossil which would justify the creation of a new genus and for biogeographical reasons we tentatively assign our fossil to the more widespread *Siro* and suggest that this genus may have inhabited Central Europe since at least the mid-Tertiary.

While most members of the Laurasian Sironidae are smaller than 1.8 mm, a few species are

reported to measure between 2.0 and 2.5 mm. Among the European species, *Siro gjorgjevici* Hadži 1933, *S. teyrovskyi* Kratochvíl 1938 and *Tranteeva paradoxa* Kratochvíl 1958 measure between 2.0 and 2.5 mm in length.

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THE MALE MATING SYSTEM IN A DESERT WIDOW SPIDER

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ABSTRACT. Competition among males is a major force shaping sexual selection. We investigated the male mating strategy of the widow spider *Latrodectus revivensis*, a desert species with an annual life cycle. Based on morphology of the sperm storage organs reported for female *Latrodectus*, we predicted that males should guard sub-adult or virgin adult females. In a natural population, we found that males were generally monogamous, cohabiting longer with sub-adult females approaching the final molt than with adult females. Nevertheless, both the duration and timing of male cohabitation were highly variable. Males were found with females from a few days before or after female maturation to over two months after maturation. Maturation of males and females peaked in spring, with a second, smaller peak in summer. Adult males that matured in spring were larger than those maturing later in the summer, while for adult females the pattern was reversed. We suggest that large males of *L. revivensis* that mature in spring maximize reproductive success by mating with virgins. Late males will gain greater reproductive success from mating with large, late-maturing females, but the scarcity of these females in the population at this season may make opportunistic mating with non-virgin females a viable strategy.

Keywords: Mating strategy, *Latrodectus*, sexual cohabitation, size dimorphism

The reproductive success of a male depends on his mating success, i.e., the number of females with whom he mates, and on the number of his sperm that successfully reach and fertilize the females' eggs. In species lacking parental care, where the male's contribution to his offspring is limited to sperm, a male's fitness can increase with additional matings. The combined selection pressures to overcome rival males and convince, force or harass females into mating will shape male behavior, morphology and physiology and affect the mating system (Andersson 1994).

A male's behavior can enhance his reproductive success. In spiders, males may guard females and engage in physical contests with rival males (Elgar 1998). Female receptivity may be reduced after mating by means of male-induced mating plugs (Jackson 1980; Masumoto 1993) and her attractiveness to additional males may be lowered by removing or reducing the female's web and thereby decreasing the surface area of silk with female

pheromone (Watson 1986). Increasing copulation duration (Andrade 1996; Elgar 1995) or the number of copulations (Bukowski & Christenson 1997) and infanticide (Schneider & Lubin 1996) are additional means of assuring male reproductive success in spiders. The male's reproductive success is influenced also by ecological factors such as the availability of females of different developmental stages (adult, sub-adult, juvenile) and reproductive status (virgin or mated), the dispersion of females, male longevity and the operational sex ratio. Thus, phenology, body size, demography and the interactions among males and between males and females can influence the opportunity for males to mate with different partners (e.g., Anava & Lubin 1993; Riechert & Singer 1995). The pattern of sperm use or sperm priority is another factor which can influence male mating success. Sperm priority may be determined in part by the morphology of sperm-storage organs. Austad (1984) suggested that in entelegyne species, which tend to have 'conduit' type spermathecae, first male sperm priority should be the dominant pattern because the first sperm to enter is the first to leave the spermatheca and to fertilize the eggs. Recent evidence, however, suggests

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that both the morphology of sperm storage organs and the pattern of sperm priority is more complex (Uhl & Vollrath 1998; Uhl 2002).

Mating opportunities, ecological factors and the pattern of sperm priority together are expected to influence male mating behavior. Pre-copulatory cohabitation and guarding of sub-adult females is most likely to occur in species with first-male sperm priority and where competition for females is intense, for example where the operational sex ratio is male biased. Post-copulatory cohabitation with adult females could be expected in species where females can mate with more than one male and particularly if there is last-male sperm priority (Eberhard et al. 1993). In cases where sperm priority is not distinct due to sperm mixing, males could cohabit with the females both before and after copulation. Alternatively males could remain with a female only long enough to court and copulate and invest instead in searching for additional females.

A number of studies attempted to correlate the type of spermatheca with mate-guarding behavior. Some comparative studies support the correlation between entelegyne species with 'conduit' type spermathecae and first-male sperm priority, and male cohabitation with sub-adult females (Jackson 1986; Eberhard et al. 1993), and others have shown male preference for sub-adult females in entelegyne spiders (Miller & Miller 1986; Toft 1989; Watson 1990; Fahey & Elgar 1997). In the widow spider, *Latrodectus revivensis* Shulov 1948 (Theridiidae), spermathecae are of the 'conduit' type (Levy & Amitai 1983) and therefore first-male sperm priority is expected. Additionally, the broken embolus of male *Latrodectus revivensis* is likely to act as a mating plug (Berendonck & Greven 2002), which could limit successful sperm transfer by later males. Furthermore, in this species, several adult males may be found simultaneously in the webs of individual females (Anava & Lubin 1993), which provides the potential for male-male competition, and thus, pre-copulatory mate guarding is predicted.

In this study, we conducted observations on a field population over three reproductive seasons and documented demographic changes likely to influence male reproductive success. In addition, we conducted a preliminary test to determine the pattern of sperm priority. Thus, we consider together the influence on

the male mating strategy of two components of intrasexual competition, namely, male competition for females and gamete competition for access to the eggs.

METHODS

Natural history.—The widow spider *L. revivensis* is found in the Negev desert of Israel (Levy & Amitai 1983). The web of *L. revivensis* consists of separate nest and prey-capture components. The nest is a densely woven cone of silk covered externally with plant parts, stones and prey remains and is constructed above ground on shrubs. The capture web includes horizontal non-sticky bridge and platform threads and vertical sticky threads that reach the ground. The diet of *L. revivensis* consists of terrestrial invertebrates: beetles, scorpions, isopods, ants and other spiders (Lubin et al. 1991, 1993).

The spiders have an annual or subannual life cycle. Adults are found throughout the summer and the mating season is from April to September. Females construct egg sacs 2–8 weeks after copulation and hatching occurs one month after egg-laying, from the middle until the end of summer. In a good season, young that hatch early in the summer can mature and complete another reproductive cycle in the same year. Eggs laid at the end of the summer hatch, but the spiderlings over-winter inside the sac and emerge only in spring of the following year. Males are smaller than females and mature faster, with 5–6 molts to adult, compared to 9–10 molts for the females. Once matured, the males leave their nests and enter a female's nest or construct a small silk shelter near the female's nest (Anava & Lubin 1993).

Field observations.—The research was conducted in the northern Negev during the years 1996–1998, in a dry wadi (riverbed) near Sede Boqer (30°52' N, 34°57' E). The vegetation is sparse and composed largely of perennial shrubs (*Zygophyllum dumosum*, *Artemisia herba-alba*, *Reaumuria hirtella*, *Helianthemum* spp., *Hammada scoparia*, *Gymnocarpus decander* and *Noaea mucronata*) on limestone hillsides. The widow spider population was monitored in an area of 25,000 m² during the spring and summer of 1996 (March–September), 1997 (March–June) and 1998 (March–August). To minimize the effect of habitat heterogeneity only spiders found in

the wadi bed and along a strip 500 meters long and 100 wide on the northwest and the south-east slopes were surveyed. Censuses were conducted every 2–4 days in 1996 and daily in 1997 and 1998. In every census the vegetation was searched for nests of juveniles, males and females. Searching for nests biases the census towards females, as nests of males are smaller and less conspicuous, and males leave their nests to search for females. The nests were flagged and the approximate location of each was noted in relation to grid markers placed along the wadi at 10m intervals. Because of differences between the years in season length, population size and phenology, data from the three seasons are analyzed separately.

Pedipalp shape and color were used to distinguish adult males from sub-adults (i.e., individuals one molt before maturation). The presence of a genital opening and the relation between leg length and body size was used to distinguish adult from sub-adult females. To follow and identify the spiders individually, the femur segment of one leg on each side was marked with water-based colors. Every adult and sub-adult male and adult female was marked, measured and released back into its nest. The two size measures taken (± 0.01 mm accuracy) were the length of two segments of the front right leg (tibia+patella) and total body length, from the anterior end of the carapace to the tip of the abdomen. To normalize the data, logarithmic transformations were performed on both leg length and body length. To analyze the change in body size in the population throughout the season, only one measure from each individual was used, taken one day after maturation or on the day the spider was found, if it was already sexually mature when first encountered.

We compared males' survival in their own nests to survival in nests of females, estimated from the field data, based on techniques described in Cox & Oakes (1984). The census data provided the dates of appearance and disappearance of each male. For some individuals the exact date of death (exact failure) was known, while others were right-censored, i.e. the animal survived at least to a particular date, but the exact date of death was not known. In our case, the failure time is within the time interval between two census events. The Kaplan-Meier estimator (Kaplan & Meier

1958), limited to right censored and exact failure data, was used to calculate the survival of males over the two stationary phases in their life, namely, in their own nests and in nests of females. The program SURVIVAL in SYSTAT 7.0 (Wilkinson 1997) was used for the analysis.

We estimated the variation in clutch size and hatching success in the field for comparison with the results from doubly mated females in the lab (see below). Empty egg sacs were collected from deserted nests at the end of seasons 1996, 1997 and 1998. We counted the total number of eggshells to estimate total clutch size and the number of unhatched eggs and dead young. Sacs with signs of predation were not included in the analysis.

Sperm precedence pattern.—To determine sperm precedence pattern we used a double mating technique with sterilized males and fertile (normal) males. There were four treatment groups of sequentially mated females: SS, SN, NS and NN, where S represents sterilized males and N represents untreated (normal) males. The females in the NN treatment were introduced to a sequence of two fertile males and the females in the SS treatment were introduced to a sequence of two sterile males. In the SN group the first male introduced to each female was sterile and the second fertile and in the NS group the first male introduced to each female was fertile and the second sterile. Males were virgins in all cases and females were virgins at the start of the experiment. The experiment was conducted at c. 24°C and under artificial light adjusted to the ambient light regime. Some of the spiders were reared in the laboratory from hatching to maturation and some were collected in the field 2–3 molts prior to maturation. The spiders were fed with live prey (fruit flies, crickets, grasshoppers and beetles). Each individual was kept in a separate container.

The experiment included 30 males and 15 females. A week to 10 days after the last molt the males of the S group were exposed to 8.3 min. of 600 RAD/min. of Cobalt 60 (a total dosage of 5000 RAD). This amount of radiation is deemed sufficient to damage the DNA of the sperm cells without appreciably affecting their mobility (Jackson 1980; Vollrath 1980; Austad 1982; Kaster & Jakob 1997). The males and their female partners and each pair's mating sequence were chosen randomly.

Table 1.—Total clutch size and proportion of eggs hatched (median and range) in egg sacs collected from nests in the field during 1996, 1997 and 1998. Data are shown only for the first four eggsacs. Sacs with evidence of predation were not included.

Year	Eggsac 1		Eggsac 2		Eggsac 3		Eggsac 4	
A. Clutch size								
1996	263	(18–390)	183	(21–513)	130	(53–623)	167	(6–203)
1997	359	(0–493)	304	(190–377)	208	(134–327)	322	(171–354)
1998	316	(18–632)	274	(40–513)	282	(53–623)	186	(140–233)
B. Hatching success								
1996	0.99	(0.25–1)	1	(0.15–1)	1	(0.89–1)	1	(0.99–1)
1997	1	(0–1)	1	(0.99–1)	1	(0.99–1)	0.99	(0.95–1)
1998	0.99	(0.2–1)	1	(0.84–1)	0.99	(0.89–1)	1	(1)
C. Sample size (Number of eggsacs)								
1996	6		11		9		4	
1997	9		5		4		3	
1998	16		10		6		2	

The first male was left in the female’s container for 5 h after which he was removed and a second male was introduced for another consecutive 5 h. In *L. revivensis* it was difficult to determine whether copulation had occurred due to the small size of the male and the color resemblance of male pedipalps and female abdomen and genital opening. Preliminary observations suggested that 5 h was sufficient to allow successful copulation. In nature, mating occurs during the day, as at night females hunt actively on their webs. Therefore, we conducted the mating experiments in the lab during the day. Males and females were measured before the experiment and each male was used only once.

The egg sacs produced by each female were numbered, and the dates of construction and hatching were recorded. The first four egg sacs of each female were opened two months after they were built, a sufficient time for all the fertile eggs to hatch. Using a dissecting microscope and a counter, we recorded for each egg sac: total number of eggs, number of spiderlings, number of eggshells and the number of unhatched eggs. Usually the number of eggshells closely matched the number of spiderlings. We used the data to determine the proportion of eggs that hatched in each treatment. Because of small sample sizes and high variability in proportion of eggs hatched between females and between different egg sacs of a single female, we have not attempted to calculate P2 values (proportion of eggs fer-

tilized by the second male to mate, Andrade 1996; Schneider & Lubin 1996), but rather we report the results as the proportion of eggs hatched and total clutch size for the first four egg sacs for all 15 females (Table 1).

RESULTS

Maturation time and survival.—Males began to mature before females (Fig. 1). The greatest number of adult males was found when half of the females in the population were still sub-adult. The number of adult females peaked between the end of April and the beginning of May, by which time the number of adult males was declining.

In 1996, only one dead male was recovered and therefore survival time could not be calculated. Fifty-two males were found, 18 in their own nests and 33 with were first found with females. Three of the 18 males (16.7 %) that were found as adults in their own nests were later discovered cohabiting with females. One of the three males moved at least 8 m to the female’s nest. Two males cohabited with two different females, moving at least 10 and 80 m, respectively, between successive females.

In 1997 we compared the survival of marked males when in their own nests with their survival once they reached the nest of a female. Of 81 adult males that were captured, marked and released, 36 (44.4%) were found initially in their own nests and 45 were encountered for the first time in a female’s nest.

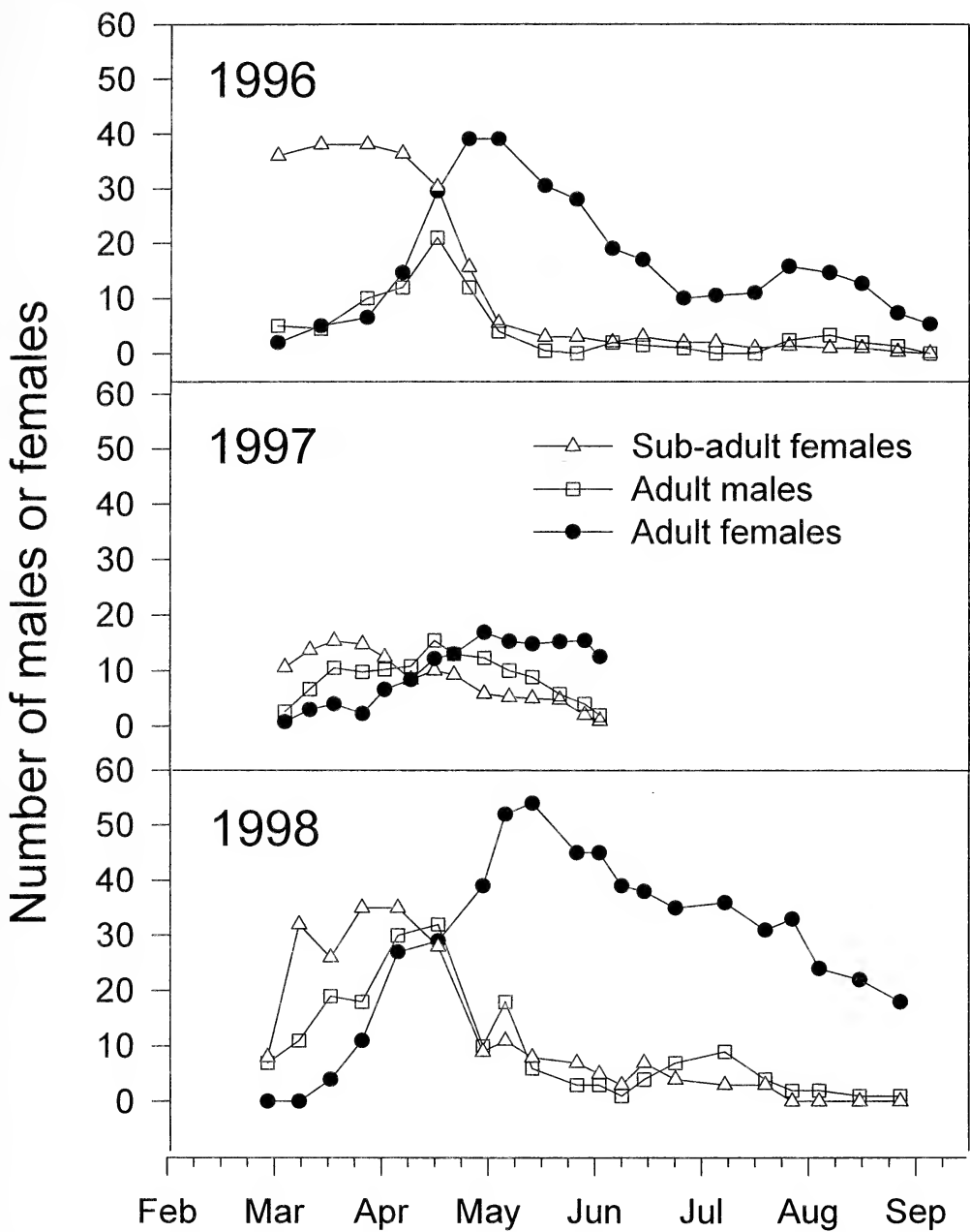


Figure 1.—Number of adult females, sub-adult females and adult males averaged over 7–10 day intervals in 1996, 1997 and 1998.

Only three males (5.6%, $n = 36$) encountered first in their own nest, were later found cohabiting with a female. These males moved a minimum of 3, 4 and 12 meters between their own nests and those of the females. Of the males seen cohabiting with females, 13% were found dead and apparently sucked dry in the females' nests. These males were most

likely cannibalized by the females. Males survived significantly longer in their own nests than when cohabiting with females (Kaplan-Meier estimation 12 days vs. 9.4 days, respectively, $\chi^2 = 8.74$, d.f. = 1, $P = 0.003$). In 1998, 103 males were marked, 52 (50.5%) of which were found initially in their own webs and the rest in webs of females.

Three of the males marked in their own webs (5.8%) were later found with females. Males survived 33.9 days in their own nests and 28.9 in nests of females (Kaplan-Meier estimation, $\chi^2 = 0.21$, d.f. = 1, $P > 0.05$).

Timing and duration of cohabitation.—

In 1996, most males were found with females around the time when the females molted to adult (Fig. 2). Nevertheless, males were also found cohabiting with females up to 70 days after female maturation. In 1997, most males were found cohabiting with females just before they matured to about a week after they molted to maturity, and some males were found with females 50–60 days following female maturation. In 1998 males were found with females up to 85 days after female maturation, especially late in the season.

In all three seasons, males tended to stay longer in nests of sub-adult females than in those of adult females (Fig. 3). The difference was significant in 1996 (Mann-Whitney $U_{10,27} = 215$, $P = 0.03$), but not in 1997 ($U_{11,42} = 270$, $P = 0.308$) or in 1998 ($U_{13,66} = 464$, $P = 0.64$). These results include cases where a male stayed in the nest even after the female had left the nest. When these cases were removed there was still a significant difference in 1996 ($P = 0.04$). The maximum time a male remained in a female's nest was 29, 35 and 42 days during 1996, 1997 and 1998, respectively.

Male and female size.—There were significant differences between the years in the body sizes of males and females (ANOVA, $P < 0.001$) and therefore, body size trends were analyzed separately for each year.

To determine if the size of females and males that matured early or late in the season differed, we regressed the means of body and leg length of individuals measured over a period of 7–10 days against the median date of that period. Median dates were used because the date of measurement was frequently not the exact date of maturation (see Methods). In all three years, males that matured later in the season were smaller than males that matured at the start of the season (Fig. 4). The decline in total length was significant in 1996 ($r = -0.865$, $P = 0.001$, $n = 11$) and in 1998 ($r = -0.56$, $P = 0.02$, $n = 18$), but not in 1997 ($r = -0.457$, $P = 0.185$, $n = 10$). Male leg length showed a similar decline in 1996 ($r = -0.813$, $P = 0.002$, $n = 11$) and 1998 ($r =$

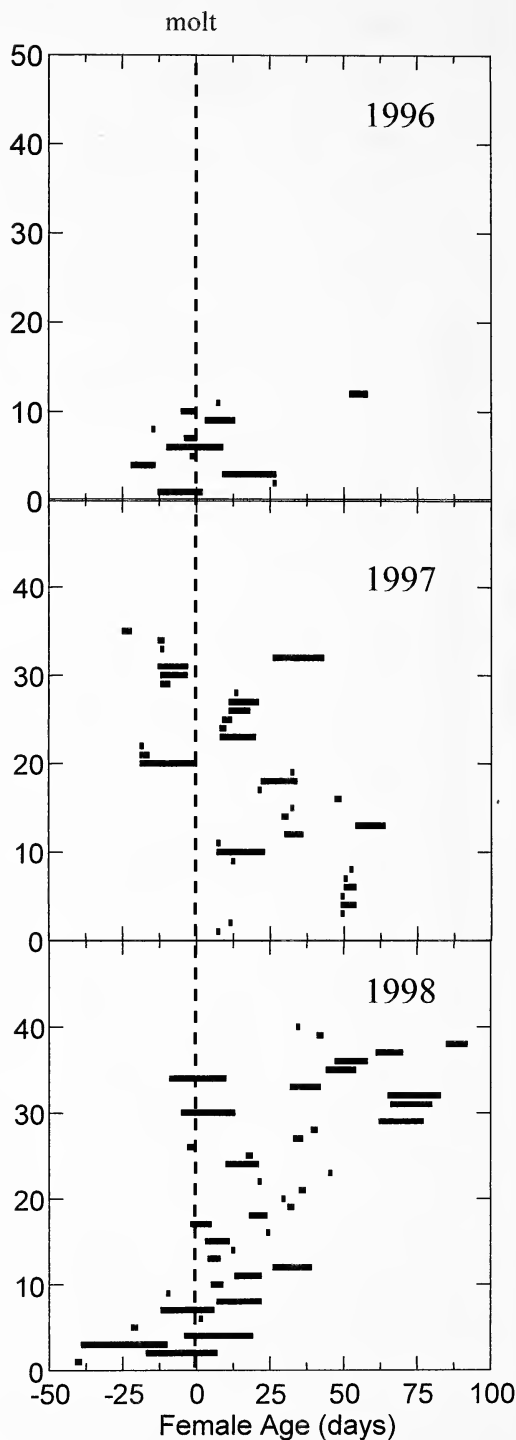


Figure 2.—Timing and duration of male cohabitation with females in 1996 ($n = 12$ males), 1997 ($n = 35$ males), and 1998 ($n = 40$ males). Individual males are arranged along the Y axis in order of their appearance from the beginning of the season to the end of the season. Female age is relative to the day of the molt to adult (day = 0).

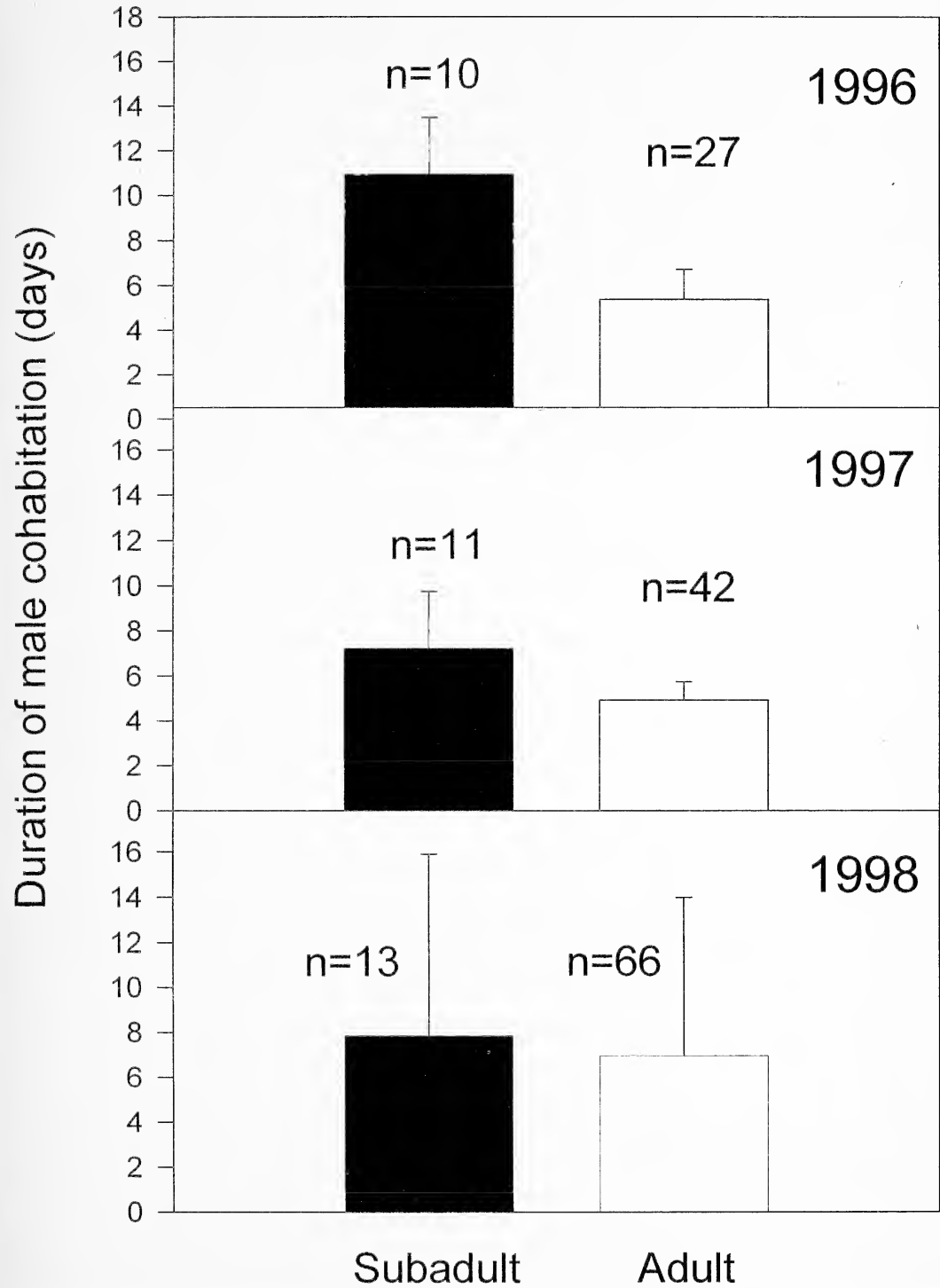


Figure 3.—Cohabitation duration in days (mean, s.d.) of adult males in nests of sub-adult and adult females in 1996, 1997 and 1998. Sample sizes are shown above the bars.

-0.52 , $P = 0.03$, $n = 18$), but not in 1997 ($r = 0.09$, $n = 10$). The change in leg lengths in 1997 was best described by a first order polynomial ($P = 0.046$, $n = 10$), showing a decrease in length from March until May.

Female size showed a trend opposite to the male size trend: both body and leg length tended to increase over the season (Fig. 4). For body length the increase was significant in 1996 ($r = -0.819$, $P = 0.013$, $n = 8$), but not in 1997 ($r = 0.508$, $P = 0.245$, $n = 7$) or in 1998 ($r = 0.329$, $P = 0.2$, $n = 16$). Leg length increased significantly in 1996 ($r = 0.819$, $P = 0.013$, $n = 8$) and in 1997 ($r = 0.793$, $P = 0.033$, $n = 7$), but not in 1998 ($r = 0.163$, $P = 0.55$, $n = 16$).

The body sizes of adult females and males found together in a nest were not correlated (Spearman rank correlation, $r_s = 0.239$, $n = 27$, $P > 0.1$; $r_s = 0.09$, $n = 35$, $P > 0.1$; $r_s = 0.024$, $n = 61$, $P > 0.1$ in 1996, 1997 and 1998 respectively). Nor was there a significant correlation between pairs of males and females for leg length or body condition index (body length/leg length) ($P > 0.1$ in all years).

A difference in size between adult males in their own webs and males found cohabiting with females could indicate female mate choice or male-male competition for females. However, when time in the season was accounted for by analysis of covariance (ANCOVA), there was no significant difference in leg length or body length of solitary and cohabiting males in 1996 (leg length: $F_{1,50} = 0.379$, $P = 0.541$; body length: $F_{1,50} = 1.028$, $P = 0.316$) or in 1997 (leg length, $F_{1,80} = 0.804$, $P = 0.373$; body length, $F_{1,80} = 0.13$, $P = 0.719$).

Mating system.—In all three years, most males visited only a single female (Fig. 5). In 1997, there were no males observed in more than a single female nest; in both 1996 and 1998, 4% of males were found in nests of two females. A greater proportion of females, however, were visited by more than a single male (Fig. 6). Five percent of females were visited by more than a single male in 1996, 28% in 1997 and 15% in 1998.

Sperm precedence.—In the field data, we found large variation in clutch size in all three seasons. The median proportion of eggs that hatched was near 1, but with considerable individual variation (Table 1).

The median proportion of eggs hatched in

the NN treatment was between 0.5 and 0.845. Eggs laid by the females mated with two sterile males (SS treatment) did not hatch at all. In both the SN and NS treatments, two females each produced 2–4 successive eggsacs with no fertile eggs, while in the other two females in each treatment, hatching proportions were variable (SN: 0.37–0.99, NS: 0.23–0.99). The clutch size of the four females that produced no fertile eggs was within the range of clutch sizes of females that did produce hatching young and of females mated to two fertile males (Table 2).

There was no significant difference in clutch size between sacs 1–4 within each treatment (Table 2, ANOVA: $F_{3,45} = 0.401$, $P > 0.05$), nor was there a difference between the four treatments (ANOVA: $F_{3,45} = 2.698$, $P > 0.05$). The proportion of eggs that hatched in successive sacs within each of the three treatments did not increase or decrease significantly (NN: $r_s = -0.370$, $n = 16$; SN: $r_s = 0.043$, $n = 15$; NS: $r_s = 0.019$, $n = 14$; Table 2) although a negative trend was seen in the NN group. We found no significant difference between the treatments in the interval between mating and egg-laying (Kruskal-Wallis, $P = 0.833$, d.f. = 3, $n = 15$) and only a small fraction of the variability in hatching proportion was explained by the interval between mating and oviposition ($R^2 = 0.045$, $P = 0.450$, $n = 15$).

DISCUSSION

Both males and females had two peaks of maturation, a larger one in spring and a small one in summer. Adults are strongly sexually dimorphic in body size and the difference in size increased as the season progressed. Thus, males that matured early in the season were relatively large, while females were small; males maturing late in the summer were small, while late-maturing females were large. Males matured before females and either remained in their own nests or joined sub-adult females in their nests. Males tended to stay longer with sub-adult females close to the time of the molt to sexual maturation than with adult females. Nevertheless there was considerable variation in the timing and duration of male cohabitation in relation to female maturation date. Adult males were seen cohabiting with sub-adult or adult females a month before and more than two months post

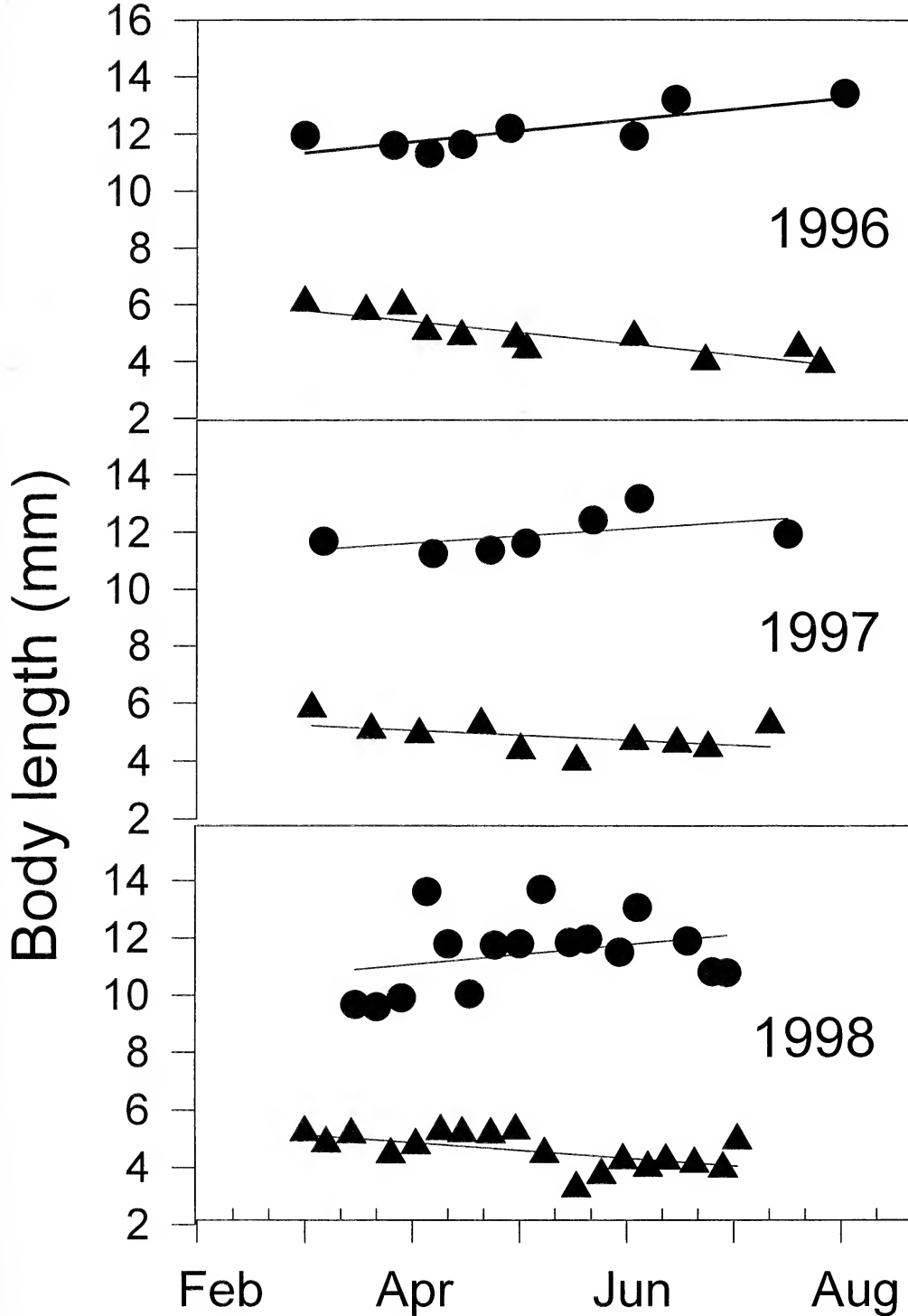


Figure 4.—Body sizes (total length, mm) of adult females (●) and males (▲) throughout the season. Regressions are of 10-day (1996) or 7-day (1997 and 1998) averages (see text). Each individual measurement was used in the regression only once, at the date the spider matured or was first encountered as an adult. There were 80 males and 33 females in 1996, 59 males and 79 females in 1997 and 103 males and 66 females in 1998.

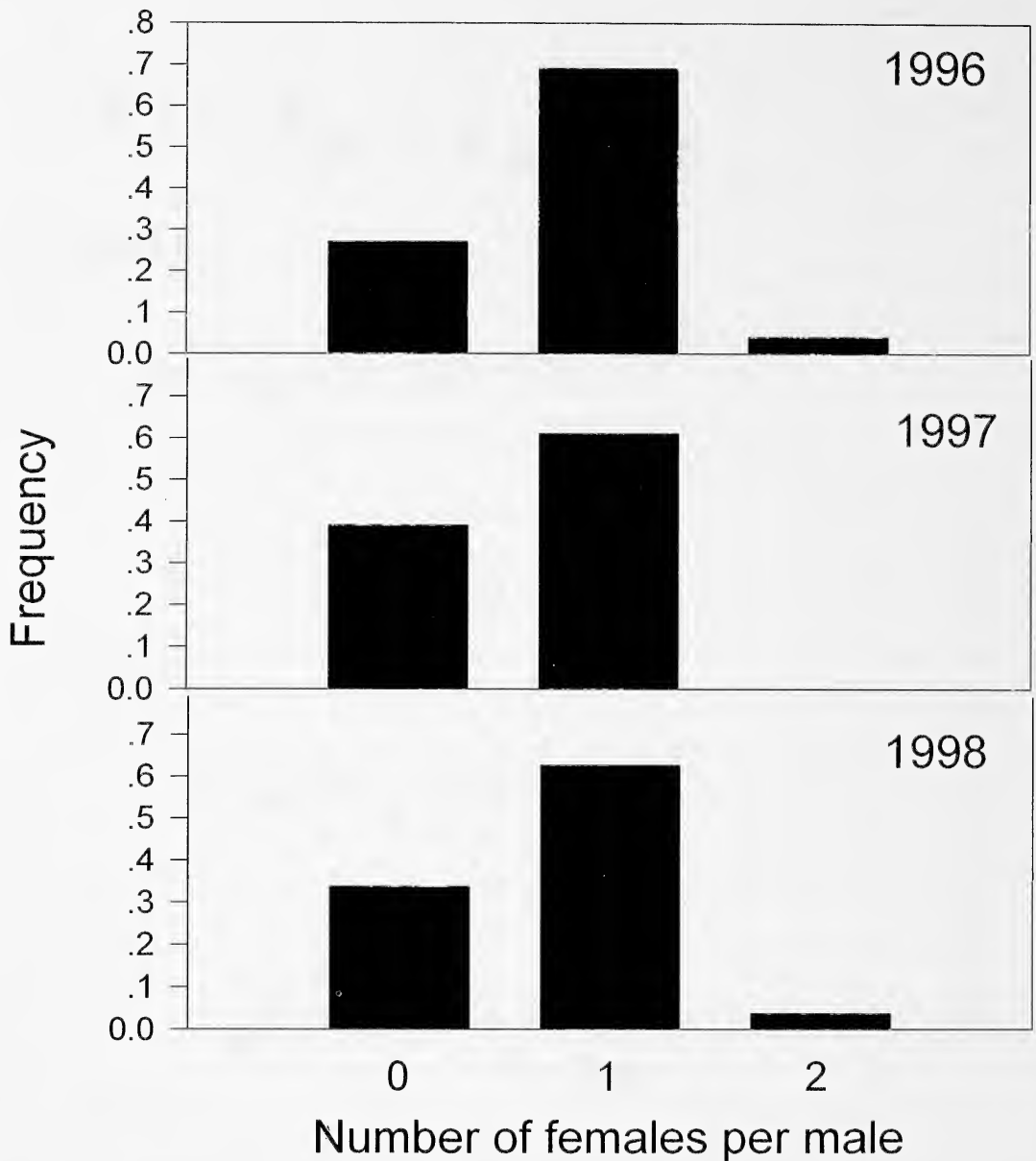


Figure 5.—Frequency distribution of the number of females that were visited by males during 1996, 1997 and 1998. Sample sizes were 81 adult females in 1996; 25 females in 1997; 99 females in 1998.

maturation, and for periods of a day to more than one month. The field data indicate that most of the males in the population were monogamous, but that females were often exposed to visits of several males.

Male monogamy.—Male monogamy is expected when the probability of encountering and mating with additional females is low (Andersson 1994; Riechert & Singer 1995). This would be the case if non-virgin females

resist additional matings (Reynolds 1996), if male mortality risks during searching or on the female’s web are very high (Vollrath 1980; Vollrath & Parker 1992; Andrade 1996) or if there are morphological or physiological constraints on multiple mating in males (e.g., loss of a pedipalp during mating; Knoflach & van Harten 2001).

In *L. revivensis* females in the laboratory, resistance to additional copulations appeared

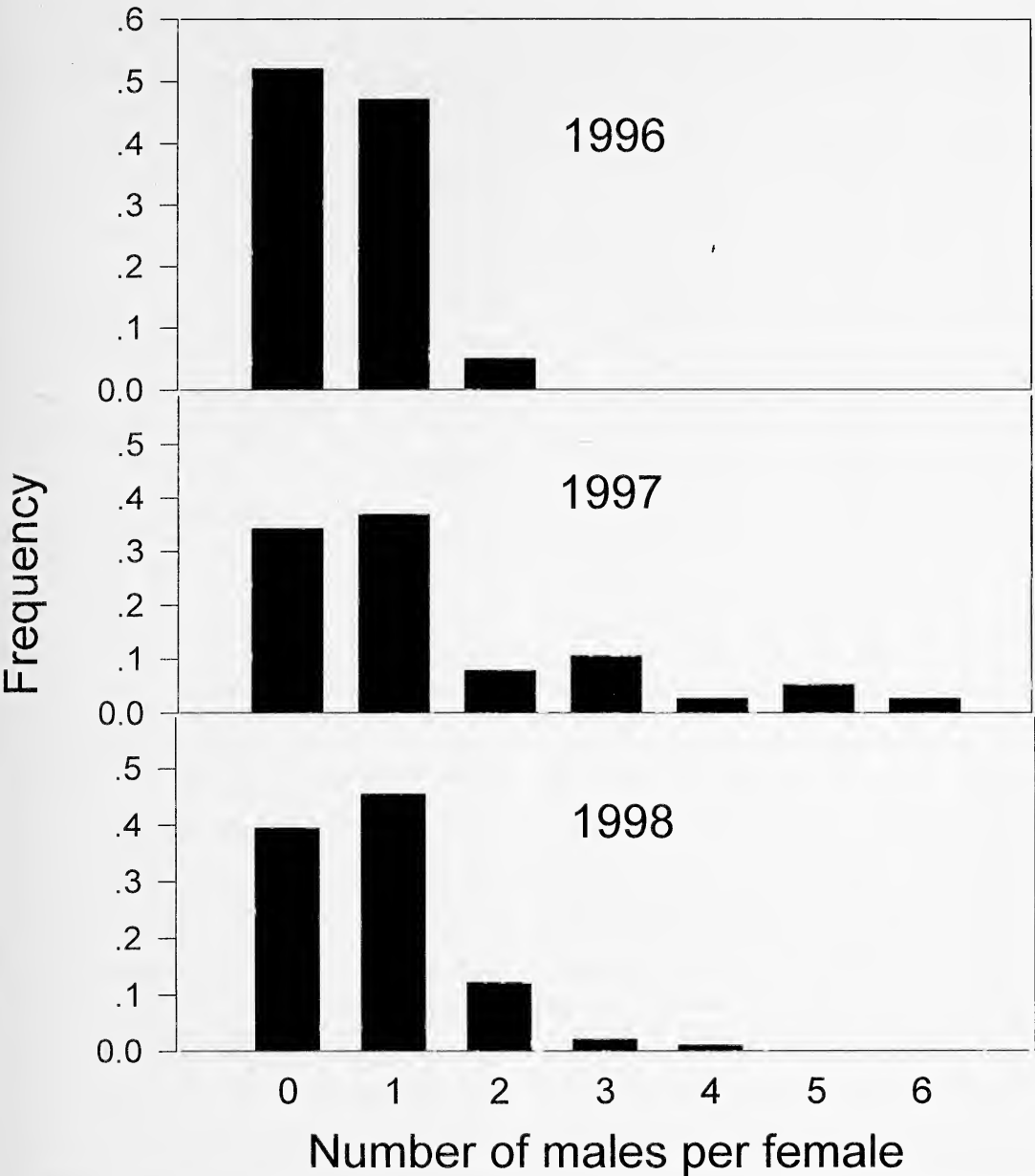


Figure 6.—The number of males that visited females’ nests during 1996, 1997 and 1998. Sample sizes were 53 males in 1996; 53 males in 1997; 58 males in 1998.

to increase with time from the first mating (pers. obs). In the field, however, we found males with females that were several weeks after their final molt, and even with females with eggsacs. Thus, mating opportunities do not seem to be restricted to virgin females. Mortality on the female’s web due to female cannibalism was not high (13%) by comparison with some other widow species (e.g, 65%

in *L. hasselti*, Andrade 1996). Thus, terminal investment of the male in a single female, as occurs in *L. hasselti*, is not expected and does not explain monogamy in *L. revivensis*. Mortality of males in their own nests was relatively low (3–6%), but very few males that were marked in their own nests were found later in webs of females in the study area (<4%), suggesting that mortality during

Table 2.—The proportion of eggs that hatched and total clutch size of four eggsacs produced sequentially. The data were collected from 46 eggsacs produced by 11 females.

Female	Treatment	Proportion hatched (clutch size)			
		Eggsac 1	Eggsac 2	Eggsac 3	Eggsac 4
1	NN	0.81 (137)	0.85 (141)	0.91 (126)	0 (46)
2	NN	0.45 (214)	0.58 (156)	0.62 (122)	0.5 (90)
3	NN	0.88 (179)	0.91 (123)	0 (190)	0.70 (187)
4	NN	0.97 (102)	0.81 (167)	0.78 (94)	—
5	SN	0.92 (167)	0.65 (180)	0.99 (145)	0.96 (142)
6	SN	0.55 (163)	0.80 (128)	0.37 (176)	0.67 (101)
7	SN	0 (151)	0 (99)	0 (176)	0 (100)
8	SN	0 (104)	0 (77)	0 (98)	0 (69)
9	NS	0.99 (192)	0.23 (119)	0.85 (141)	—
10	NS	0.35 (139)	0.98 (292)	0.97 (234)	0.91 (160)
11	NS	0 (169)	0 (177)	0 (144)	0 (110)
12	NS	0 (223)	0 (156)	—	—
13	SS	0 (146)	—	—	—
14	SS	0 (244)	0 (285)	0 (203)	0 (209)

searching for females could be high. In juvenile and sub-adult females, 40% of spiders on average were estimated to have died during the movement phase of web relocation (Lubin et al. 1993). Alternatively, marked males may have moved out of the study area to find females elsewhere, while the unmarked males that appeared in nests of females were likely immigrants from outside the census area. The large distances moved by marked males (up to 80 m) support this idea. Furthermore, if males are attracted directly to webs of recently molted females by means of volatile pheromones in the female web silk (Schulz & Toft 1993; Miyashita & Hayashi 1996; Papke et al. 2001), then the high mortality typical of random mate search would be eliminated or reduced. Thus, it is possible that male monogamy is not due to costs of mating dispersal in this species.

Levi (1959) observed that male *Latrodectus* often lost the tip of the embolus, and emboli could be found inside the spermathecae of females, suggesting that the embolus may act as a mating plug. This idea has received support from a recent morphological study (Beren-donck & Greven 2002). If males who have lost an embolus tip are unable to re-charge the palp, or are unable to deliver sperm to the spermatheca, then a male could successfully copulate only twice. Thus, if a male copulated twice with the same female, he would be effectively monogamous. This explanation for

finding marked males in the field with at most two females remains to be tested.

Cohabitation.—Based on spermathecal structure, we predicted that *L. revivensis* should have first-male sperm priority and that males should attempt to mate with virgin females (Austad 1984). As a corollary, we predicted mate guarding of sub-adult females nearing maturation. Some cohabitation with sub-adults occurred in our field population, but most cohabitation occurred just after the female’s molt to maturity. Preliminary data show that males are not attracted to silk from webs of sub-adult females, and that this silk lacks some volatile compounds present in webs of recently molted adult females (Lubin & Papke unpubl. data). Furthermore, sub-adult females often shifted to a new website within a few days of a male arriving at the nest (Lubin et al. 1993), which suggests that sub-adult females are not always tolerant of the male’s presence. Thus, a strategy of searching for and guarding sub-adult females until they molt may be less rewarding than seeking adult virgin females. Recently molted females attract males from several meters away (unpub. obs.). Another apparently anomalous behavior is explained in this context: we found that after molting to maturity, males often remained in their own nests for very long periods; up to 42 days. They do not feed during this time and thus should lose both body mass and potential mating oppor-

tunities. The behavior can be understood, however, if males remain in their nests until the pheromone of a female is detected, and then move rapidly towards the source. Such a movement strategy would also minimize the risk of mortality associated with random searching. To our knowledge, this prolonged delay between maturation and leaving to search for females has not been noted in other studies.

Sperm precedence.—The pattern of hatching success in the double-mating experiment would suggest sperm mixing. However, problems emerged with the sterile male technique of assessing sperm priority, and consequently we are unable to define the pattern of precedence. First, as we did not observe the pairs continuously during the 5 hours that each male was left with a female, we could not be sure that copulation had indeed occurred. Second, even if the male copulated, he may not have transferred sperm. Bukowski & Christenson (1997) examined sperm remaining in male pedipalps and showed that sperm transfer does not always take place in spiders even when the pair copulate. If male *L. revivensis* consistently break off the terminal sclerite of the embolus during copulation (Levi 1959; Berendonck & Greven, 2002), it may be possible to determine if a male copulated successfully by examining the male palps after mating for the loss of an embolus tip or, alternatively, by counting sperm in the pedipalps (Bukowski & Christenson 1997; Schneider et al. 2001). Finally, a male may copulate with one or both palps, filling one or both of the female's spermathecae. If the broken embolus tip acts as a partial or complete barrier to further sperm transfer, then we should expect a strong first male priority effect as a consequence of pre-copulatory 'sperm' competition. In the SN treatment in our experiments, two females produced a succession of completely infertile clutches. This could be explained by the presence of embolus tips of the sterile (first) male, which blocked both spermathecae, and thus not allowing the fertile (second) male to inseminate the female. However, similar failures occurred in two females in the NS treatment, an observation which is difficult to explain. Clearly, further experiments remain to be done to investigate the relationship between mating sequence and sperm priority.

Male mating strategy.—Several features which may be under direct or indirect sexual selection are evident in the male mating strategy of *L. revivensis*. These include: protandry, male body size, searching and cohabitation with adult and sub-adult females. Protandry, or early maturation of males, is common in spiders and other arthropods, and is often thought to increase chances of obtaining females, particularly under scramble competition (mate opportunity hypothesis; Morbey & Ydenberg 2001). If a broken embolus indeed acts as a mating plug and female re-mating is limited, then protandry in this species may be selectively advantageous to males.

Linked to protandry is the large sexual size dimorphism and seasonal variation in male body size. Males mature at an earlier instar than females, while selection on fecundity presumably favors large body size and hence later maturation in females (Lubin et al. 1993). However, the relative timing of maturation, and the resulting body sizes, differ for individuals that mature in spring and those maturing later in the summer. Males that mature in spring have had 6–8 months to grow, assuming they hatched in the autumn, while summer maturing males are from eggs that hatch in spring and have only 3–4 months of growth from hatching to maturation. Thus, spring maturing males are large and in good body condition and summer maturing males are small. Spring maturing females, however, are small relative to summer maturing ones, as food supplies, particularly of large arthropods that constitute the main prey of females (Lubin et al. 1993), are more abundant in the summer months. These observations suggest that there are different selective forces acting on maturation time and body size in males and females. In males, sexual selection promotes early maturation for both development peaks (spring and summer). For spring females, early maturation is also advantageous, because their young will hatch in spring or early summer when insects are most abundant. Thus, spring maturing females are relatively small, while summer females (that produce overwintering young) are not constrained by timing of maturation and fecundity selection will be manifested in larger body size.

The above decisions relating to the timing of maturation and their effects on body size of males and females, have further conse-

quences for male behavior. In spring there are many virgin females and males can adopt one of two search strategies: high-risk random search and cohabitation with sub-adults or low-risk directional movement to webs of newly-molted virgins, where they face competition from other males (Anava & Lubin 1993). Large body size is likely advantageous in male-male competition (Elgar 1998). As the reproductive season progresses, virgin females are sparsely distributed in time and space. Male search strategy may shift to attempting to mate with non-virgin females when the chance of finding a virgin female is low. Observations of males in nests of females that were many weeks post-maturation support this idea. We have also observed males attempting to copulate opportunistically with a female that already had egg sacs and was engaged in feeding on large prey. Whether mating with older females is a distinct male mating 'strategy' or a case of late-maturing males making 'the best of a bad job' is not clear. Nevertheless, late males have one advantage in that late females are large and have high fecundity and thus may have greater reproductive success than early males. In summary, the male mating strategy appears to be a flexible outcome of the interaction between seasonal growth decisions, availability of potential mates and possible morphological constraints.

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THIRD SPECIES OF GUASINIIDAE (OPILIONES, LANIATORES) WITH COMMENTS ON FAMILIAL RELATIONSHIPS

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ABSTRACT. *Guasinia persephone*, a new species of the family Guasiniidae, is described from the soil of an inundation forest in Brazilian Amazonia. This family was hitherto only known from two species from Venezuela. Male genitalia of the new species are described in detail. A close relationship of Guasiniidae with Zalmoxidae and Fissiphalliidae is proposed on basis of genital morphology. This is the third species of blind Laniatores from Brazil and the first from leaf mold, one is from termite nests and the other is from a cave.

Keywords: Guasiniidae, Neotropics, Opiliones, anophthalmy, Brazil, Amazonia, Arachnida

The family Guasiniidae (correct spelling for a family name based on the generic name *Guasinia* González-Sponga 1997, see Kury & Pinto-da-Rocha 2002) is the most recently discovered family of Laniatores (González-Sponga 1997). The other recently described families are Fissiphalliidae Martens 1988 and Agoristenidae Šilhavý 1973 from the Neotropics and Pentanychidae Briggs 1971 from the Nearctic. González-Sponga (1997) provided descriptions of two monotypic genera of Guasiniidae, with only very schematic drawings of the penis of both species and related them to the Oriental family Oncopodidae Thorell 1876.

Guasiniidae, together with Fissiphalliidae and Ogoveidae, both with three described species, are the least diverse families among Opiliones. According to Roewer's system, which dominated the past 90 years of Opiliones systematics, guasiniids should be included in the "wastebasket" family Phalangodidae Simon 1879. However, as distinct from members of the Fissiphalliidae, which are externally very similar to zalmoxids, Guasiniidae were described on well-delimited external characters. It can be reasonably expected to find Fissiphalliidae described among the Phalangodidae of Roewer, however it is highly improbable that a guasiniid has been described previously in Phalangodidae or another family due to the striking structure of the pedipalps, as well as the minuscule body

size and the strictly defined microhabitat. The recognition of the Guasiniidae (González-Sponga 1997) was a welcome departure from the conservative approach by the same author (González-Sponga 1987), who preferred to keep the polyphyletic family Phalangodidae, discarding the use of Minuidae and Zalmoxidae.

The discovery by Dr. Joachim Adis (Max-Planck Institute, Plön, Germany) of new material from upper soil layers near Manaus (Central Amazonia) is here described as a new species. This minute opilionid expands the distribution range (recorded only from Venezuela) of the family Guasiniidae much southwards and offers the opportunity to illustrate and discuss the male genitalia and attempt to relate this family to other laniatorid families.

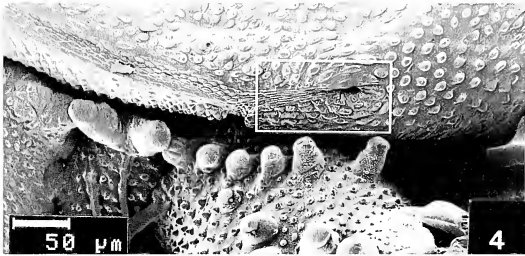
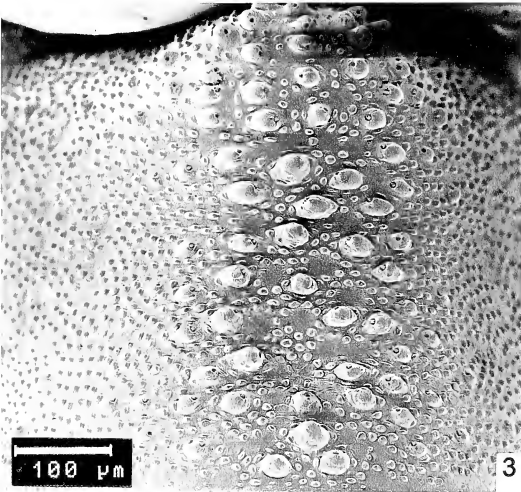
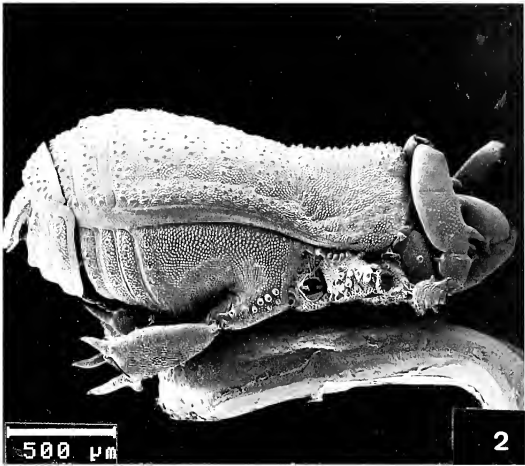
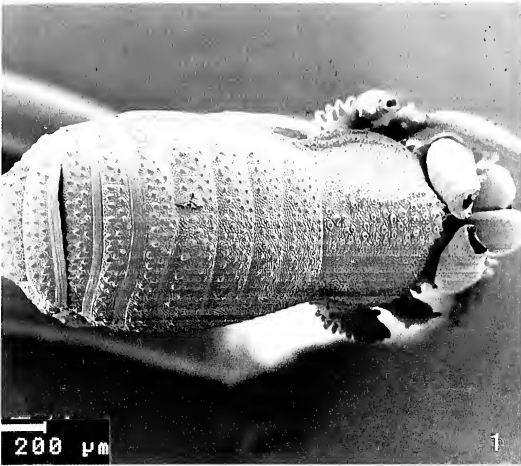
The material studied is deposited in the Instituto Nacional de Pesquisas da Amazônia (INPA, C. Magalhães); Museu de Zoologia da Universidade de São Paulo (MZSP, R. Pinto-da-Rocha), Museu Nacional do Rio de Janeiro (MNRJ, A.B. Kury) and Senckenberg Museum (SMFD, M. Grasshoff).

SYSTEMATICS

Family Guasiniidae González-Sponga 1997

Genus *Guasinia* González-Sponga 1997
Guasinia González-Sponga 1997: 53.

Type species.—*Guasinia delgadoi* González-Sponga 1997, by original designation.



Figures 1–5.—*Guasinia persephone* new species, male: 1, Habitus, dorsal view; 2, Same, lateral view; 3, Carapace, dorsal view; 4, Right ozopore and dorsal surface of coxa II; 5, Detail of ozopore, scale 4 times larger than Fig. 4.

Emended diagnosis.—Stridulatory apparatus on mesal surface of cheliceral hand. Tarsal counts 3–4(2)/4–8(2–4)/5/5–6 (see remarks). *Guaiquinimia* González-Sponga 1997 differs from *Guasinia* by the very stout smooth and spined basichelicerite with backwards projection, and 13 segments on tarsus II.

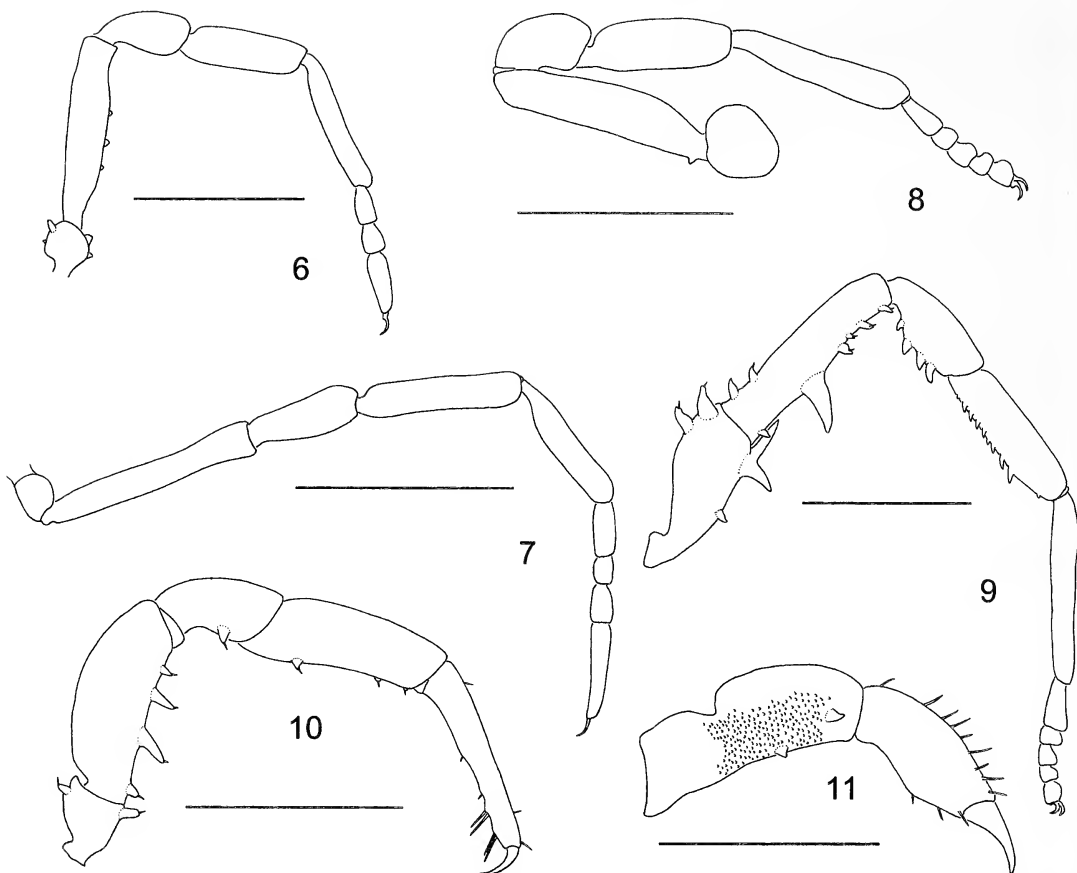
Remarks.—As currently understood, there is little reason to separate both guasiniid genera, but a synonymy would be premature at this stage.

Guasinia persephone new species
Figs. 1–15

Type material.—All material collected by Joachim Adis from Igapó Tatumã Mirim, Ma-

naus, State of Amazonas, Brazil (03°02'S, 60°17'W). Holotype male, date 26 July 1983, (INPA). Paratypes: 23 February 1982, 1 ♀ (INPA); 1 ♂ (MNRJ); 1 ♀ (INPA); 29 September 1982, 2 ♀ (INPA); 1 ♀ (SMFD); 25 March 1983, 1 ♂ (SMFD); 28 March 1983, 1 ♀ (MZSP); 1 ♂ (MNRJ); 25 April 1983, 2 ♂, 3 ♀ (MNRJ); 2 ♀ (INPA); 2 ♀ (SMFD); 1 ♂ (MZSP); 26 May 1983, 2 ♂, 2 ♀ (INPA); 27 June 1983, 3 ♀ (INPA); 1 ♂ (MZSP); 24 July 1983, 1 ♀ (INPA); 26 July 1983, 1 ♀ (INPA); 2 ♂, 1 ♀ (MZSP); 3 ♀ (MNRJ); 24 August 1983, 2 ♂, 3 ♀ (MZSP); 1 ♀ (MNRJ); 2 ♀ (SMFD); 2 ♀ (INPA).

Etymology.—The species name is treated as a noun in apposition to Persephone, a



Figures 6–11.—*Guasinia persephone* new species, male: 6, Leg I; 7, Leg II; 8, Leg III; 9, Leg IV; 10, Pedipalp; 11, Chelicera. Scale bars = 0.5 mm.

Greek goddess who was kidnapped by the god Hades (not Adis) and had to live with him in the underground realm all her life.

Diagnosis.—Differs from *G. delgadoi* by the male metatarsus II undivided and armature of leg IV with large tubercles (Fig. 9). Carapace without posterior convexity. Tarsal counts 3(2), 4(2), 5, 5. Segmentation of tarsi I–II and IV is lower than *G. delgadoi* that possesses 4(2), 8(4) on legs I–II and 6 on leg IV (see remarks). Transverse grooves of carapace I–V well defined (Fig. 1), differing from the other species of the family.

Description.—Measurements (holotype, in mm): Dorsal scute length 1.3; cephalothorax length 0.5; mesotergum width 0.8; cephalothorax width 0.65. *Dorsum* (Figs. 1–2): Outline of scute attenuate hourglass-shaped. All scutal grooves transverse and well marked. Scutal areas I–V and free tergites I–III densely covered with large granules. Carapace densely

covered with minute granules, and a stripe of coarse granules in the middle region (from anterior margin to groove I). Eye mound ill-defined (Fig. 3); eyes completely lacking. Only one transversal slit-like ozopore in lateral position (Figs. 4, 5).

Chelicera (Fig. 11): Cheliceral hand with stridulatory apparatus formed by numerous granules on mesal surface and two larger mesal teeth. Hand not inflated, similar in both sexes.

Pedipalp (Fig. 10): Coxa and trochanter with mesal field of numerous granules. Trochanter with one ventral and one basal setiferous tubercles. Femur with curved prolateral subapical tubercle, ventral row of four tubercles. Patella with mesal subdistal tooth. Tibia with three small setae on each side. Tarsus with small setae, plus longer distal setae. Claws short.

Legs (Figs. 6–9): Legs I–IV finely granu-

lated. Coxae I–IV with stout tubercles. Trochanter I with two ventral and two dorsal tubercles; femur III with one short dorsal subapical tubercle; trochanter IV with two ventral (apical much larger, bifid, forming a straight angle) and two large dorsal (posterior longer) tubercles; femur IV with two short dorsal sub basal, one short ventral sub basal, one longer than femur diameter on ventro-median followed by four short tubercles; patella IV with four ventral tubercles increasing in size; tibia IV with nine ventral tubercles increasing in size and one ventral subapical tubercle. Metatarsus II undivided. Tarsal segmentation: 3(2), 4(2), 5, 5.

Male genitalia (Figs. 12–15): Ventral plate modified as apical portion of truncus separated from the shaft by a constriction; lateral margins of ventral plate twisted around the main axis of truncus and are fused to each other, resulting in a funnel-shaped calyx; ventral plate with two groups of setae; basal group formed by 3 + 3 large foliaceous-spatulate setae with rounded apex; distal group is formed by 2 + 2 small cylindrical acuminate setae; distal portion of truncus proximal to ventral plate depressed forming a cavity where glans structures are inserted; accessories of glans well developed as a membranous sac projected into two paired lobes (titillators); conductors and other parastyli absent, stylus free.

Female: Measurements (INPA, 29.September.1982, in mm): Dorsal scute length 1.2; cephalothorax length 0.5; mesotergum width 0.8; cephalothorax width 0.65. Similar to male except as follows: cephalothorax less tuberculate. Legs with fewer and shorter tubercles; legs I–III granulate; trochanter IV with 2 single branched tubercles on ventral and dorsal; femur IV with 1 sub-basal, 1 median and 1 subapical short tubercles; patella IV with 1 ventroapical tubercle. Tarsal segmentation: 4(2), 4(2), 5, 5.

Habitat.—All of the material was obtained from inside the soil, similar to the species described by González-Sponga (1997), who found guasiniids inside bark under litter. The type locality, Taramã-Mirim, is an inundation-forest of black-water, also called igapó. The type-locality is on the lower course of the Taramã-Mirim river near the mouth of Rio Negro, 20 km upstream from Manaus, in Central Amazonia. The soil A-horizon is 10–15 cm

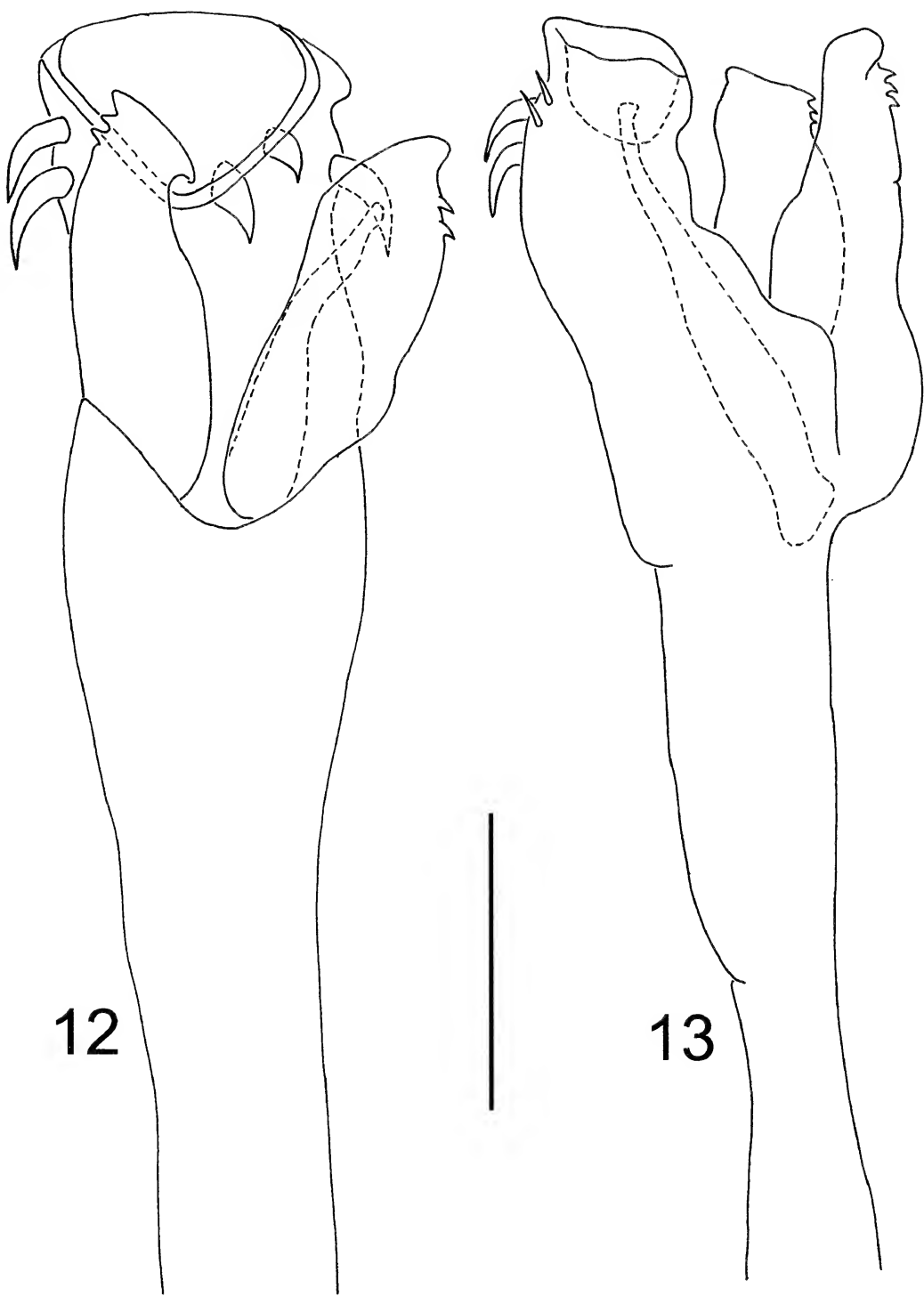
deep (humus layer = matting of humus with fine humus). The humus stratum is slightly developed (covering 5%), seedlings of abundant trees occur in large numbers, shrubs are absent, there are 1300–2000 trees/ha, totaling 47 species. The tree roots spread as far as 8 m on the forest floor. Annual precipitation ranges between 1000–2500 mm (lowest monthly precipitation 0–60 mm). Rainy months January–April; dry months July–September temperature between 24.3–27.4°C. The igapó is annually flooded for 5–6 months. The water level fluctuations are between 5.5–14 m, mean 10 m (see Adis 1981).

Remarks.—The tarsal counts of leg II of the two Venezuelan species provided by González-Sponga (1997) are not compatible with his own drawings. González-Sponga (1997) stated that *G. delgadoi* had 7(3) segments (González-Sponga 1997: 55) and that *Guaiquinimia longipes* had 10–12(4) segments (González-Sponga 1997: 58), although the drawings (his figs. 6 & 13) clearly show 8(4) and 13(3), respectively. Male genitalia of the new species appear at first to be incompatible with González-Sponga's drawings, which lack the large basal setae of the ventral plate. Our own observation is that even if those setae are very large, they are flattened and applied against the truncus, so their presence is easily overlooked using an optical microscope, reconciling penial morphology of *G. persephone* with both Venezuelan species.

DISCUSSION

This is the third anophthalmic Brazilian species of Opiliones. The first totally blind Brazilian opilionid to be described was *Caecobunus termitarum* Roewer 1927 (originally in Phalangodidae, but family uncertain, see Kury 2003), described from termite nests in Rio de Janeiro state. The second was the cave-dweller *Giupponia chagasi* Pérez & Kury 2002 from Bahia state (Pérez & Kury 2002). The other two species of Guasiniidae described by González-Sponga (1997), *Guasinia delgadoi* and *Guaiquinimia longipes* are also eyeless.

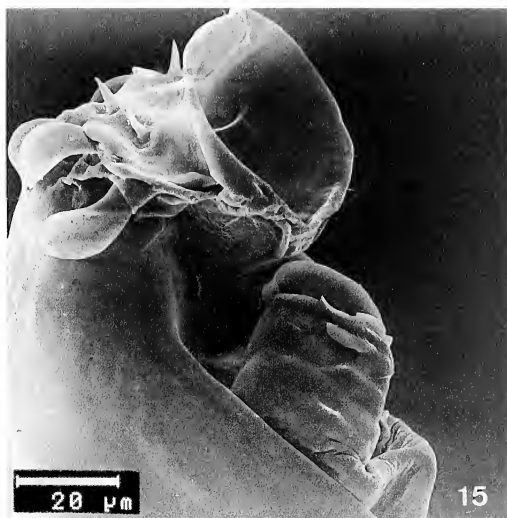
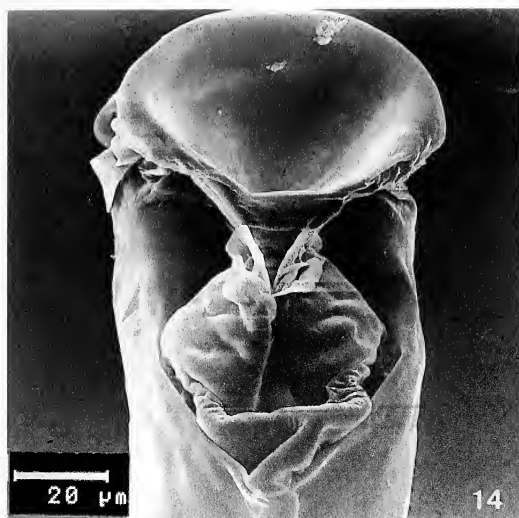
The presence of well-developed accessory of glans (Figs. 12–15) forming a solid unfoldable bifid plate articulated with the truncus relates Guasiniidae with the Zalmoxidae, Fissiphalliidae and Icaleptidae (Kury & Pérez 2002). The short pedipalpal claw, tarsus twice



12

13

Figures 12–13.—*Guasinia persephone* new species, penis: 12, Dorsal; 13, Lateral. Scale bar = 0.1 mm.



Figures 14–15.—*Guasinia persephone* new species, Distal portion of penis: 14, Dorsal view; 15, Lateral view.

as long as tibia and tarsus with reduced ventral setae seem to be autapomorphies of the family (Fig. 10). González-Sponga (1997) noticed the similarity of the pedipalps of Oncopodidae and Guasiniidae. But on closer examination, Oncopodidae have a very different somatic and genital morphology, possessing a huge glans that folds against the truncus and many somatic autapomorphies (see Martens 1986; Schwendinger 1992). In the absence of other putative synapomorphies to unit both families, this similarity between the structures of their pedipalps can be only homoplasious. The calyx formed by the ventral plate also occurs in some Caribbean species that are currently in the Stygnommatidae (Abel Pérez, pers. comm. 2002).

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LYSSOMANES (ARANEAE, SALTICIDAE) IN OLIGOCENE-MIOCENE CHIAPAS AMBER

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ABSTRACT. The genus *Lyssomanes* (Salticidae) is recorded and described from a fossil in 20–30 Ma Oligocene–Miocene amber from Chiapas, Mexico for the first time. This is the oldest described *Lyssomanes* and extends the known geological range of the genus by approximately 10 Ma from the previously oldest known specimens in Dominican Republic amber. The geological age of the family may be young compared to other extant spider families.

RESUMEN. El genero *Lyssomanes* (Salticidae) es descrito y registrado por primera vez incluido en el ámbar de Chiapas, México, tomando en cuenta una edad de 20 a 30 Ma (Oligoceno-Mioceno). Éste es el registro más antiguo que se tienen de *Lyssomanes* y con esto se extiende el rango geológico conocido para el género por aproximadamente 10 Ma de los especímenes previamente conocidos y más antiguos del ámbar de la República Dominicana. Geológicamente la edad la familia puede ser joven comparado con otras familias existentes de arañas.

Keywords: Fossil, jumping spider, Cenozoic, Mexico

Poinar & Poinar (1994) provide an interesting historical account of Mexican amber. Biological inclusions in Chiapas, Mexican amber were rediscovered, somewhat accidentally in 1952 and an expedition was launched by scientists from the Department of Entomology and Parasitology, University of California, Berkeley, to collect specimens and geological data for the deposits (Hurd et al. 1962). Twelve spiders from this collection were described by Petrunkevitch (1963), which he placed in seven extant families. Petrunkevitch (1971), published posthumously with additional notes by Harriet Exline, described ten species from 14 specimens in five extant families. Wunderlich (1986, 1988) synonymised some of Petrunkevitch's fossil genera with extant taxa, and considered the specimen identified as Dysderidae by Petrunkevitch (1971) as a dubious identification, but gave no reason for doing so. It is unclear whether Wunderlich examined the Mexican material or derived his conclusions from the descriptions alone. One partially preserved salticid was described from this amber

by Petrunkevitch (1971) but it was not possible to ascribe it to genus due to its incompleteness. Here, we describe the first identifiable salticid from Mexican amber, which belongs in the extant genus *Lyssomanes*.

Fossil *Lyssomanes* were first reported from Miocene Dominican Republic amber by Cutler (1984) and Reiskind (1986) and described by Wunderlich (1986, 1988) and Reiskind (1989); see also the synonymy of Penney (2001). Extant *Lyssomanes* are abundant in the Neotropics (e.g. Galiano 1980, 1984) with more than 60 species recorded; at least 14 species are known to occur in Mexico and one reaches north into the US (e.g. Platnick 2002). However, this genus is poorly studied in Mexico and the number of species present is probably greater than that observed (Galiano 1980). Extant *Lyssomanes* are usually translucent green, active hunters often seen stalking their prey on plant foliage and are able to jump considerable distances. They can easily be distinguished from most salticid spiders by having their eyes arranged in four rows rather than three, and they differ from other salticids with four eye rows, by the presence of dorsal

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Figures 1–2.—*Lyssomanes* sp. indet., juvenile, 5964 IHNE, in Oligocene–Miocene, Mexican amber: 1. Photograph, dorsal view; 2. Camera lucida drawing. Scale bars = 1 mm.

spines on the patellae and ventral leg spines (Galiano 1998).

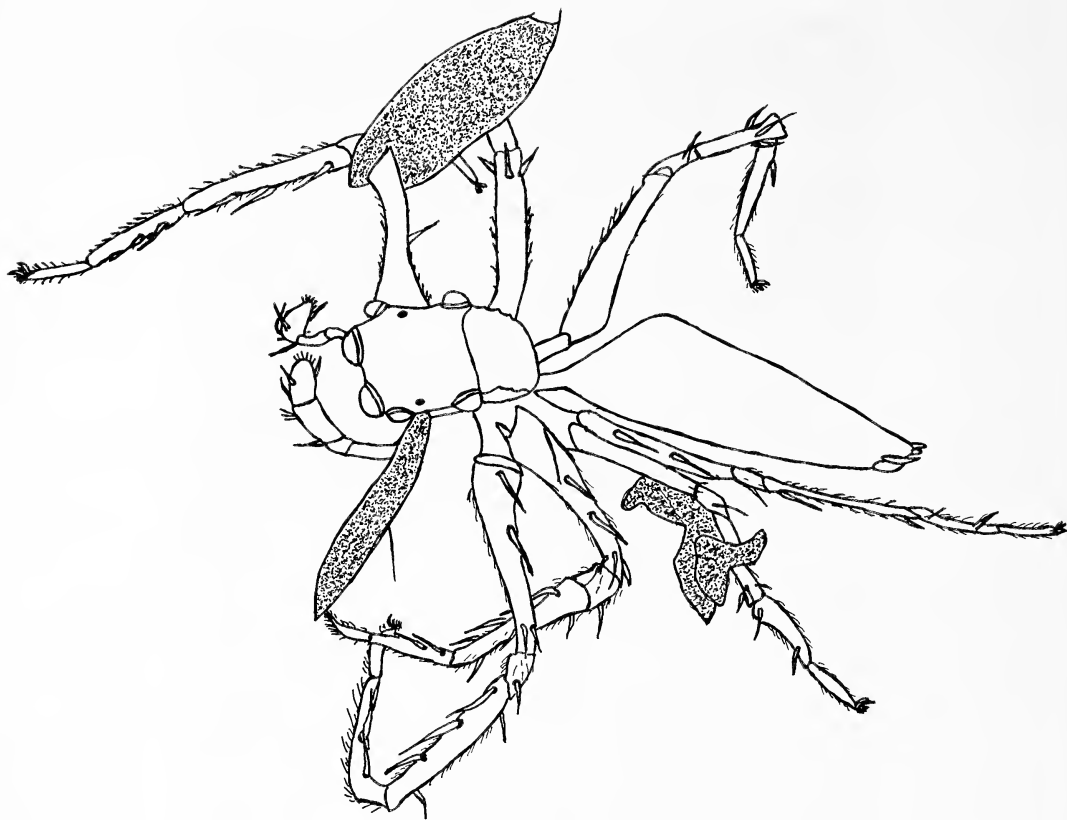
METHODS

The specimen is deposited in the Museum of Paleontology of the Instituto de Historia Natural y Ecología (IHNE) and was acquired on 30 October 2001 directly from the amber miners in Simojovel, Chiapas. All measurements are in mm and were made using an ocular graticule. Leg spination notation as in Galiano (1984). Abbreviations: d = dorsal, r = retrolateral, p = prolateral, v = ventral. Photography was with a Canon EOS 500N camera attached to a Zeiss Stemi 2000C microscope.

Lyssomanes sp. indet.
Figs. 1–2

Material examined.—Juvenile, 5964 IHNE, in Oligocene–Miocene amber from Chiapas, Mexico, examined by MAG-V.

Description.—Total length 2.68; carapace length 0.99, with short setae dorsally. Clypeus high, chelicerae moderately large and robust, marginal dentition cannot be distinguished. Eight eyes in four rows, typical and diagnostic for the genus. Sternum small, wider in front than behind. Opisthosoma length 1.69 cylindrical, as shown in Figs. 1 & 2, and characteristic of the genus; two pairs of spinnerets, which appear flattened, visible terminally. All



Figures 1-2.—Continued.

coxae are more or less cylindrical, large, and close together. All legs long and relatively thin. Leg formula: 1+2,3+4; leg 1 fe 1.0, pat-tib 1.3, mt 0.7, ta 0.4, total 3.4; leg 2 fe 1.0, pat-tib 1.3, mt 0.7, ta 0.4, total 3.4; leg 3 fe 1.0, pat-tib 1.0, mt 0.7, ta 0.3, total 3.0; leg 4 fe 1.0, pat-tib 1.0, mt 0.7, ta 0.3, total 3.0. Leg spination: femora 1 and 2 d 1-1-1, r 0-0-1, p 0-0-1; 3 d 0-0-1, p 0-0-1, r 0-0-1; 4 d 0-1-1, patellae 1-4 d 0-0-1, tibiae 1 and 2 d 1-0-1, v 2-2-2; 3 and 4 d 1-0-1, p 0-0-1, r 0-0-1; metatarsus 1 v 2-2-2; 2 v 2-2-2; 3 p 0-0-1, r 0-0-1; 4 p 1-0-1, r 1-0-1. The pedipalp is somewhat compressed, the spider may be a subadult male. There is one Diptera syninclusion.

DISCUSSION

The ambers of Mexico and the Dominican Republic are approximately contemporary and are thought to have occurred in similar settings (Grimaldi 1996). The amber-producing tree in both instances belongs to the extant genus *Hymenaea* (Leguminosae) although

different species were involved in each case (Langenheim 1995). The Mexican amber occurs in lignites and associated marine sandstones; pollen analysis suggests they were deposited in a complex of mangrove vegetation in a shallow sea environment (Langenheim 1995). Dominican Republic amber also occurs in marine sandstones with lignitic lamellae, which were also deposited in a nearshore context, probably in coastal lagoons (Itturalde-Vinent & MacPhee 1996). The Dominican Republic amber spider fauna is well known (e.g. Wunderlich 1988) and is very similar to the Recent Neotropical fauna (Penney 1999). It is not unreasonable to expect the same to be true for the Mexican amber fauna but further work on both fossil and Recent Mexican faunas is required to confirm this. We place this specimen in *Lyssomanes* because it has the following combination of characters diagnostic of the genus: eyes in four rows, dorsal patellar spines and ventral tibial spines on the anterior legs (e.g. Galiano 1998). This is the oldest recorded fossil *Lyssomanes* and extends the

known geological range of the family by approximately 10 Ma from the previously oldest described fossils in Miocene Dominican Republic amber (e.g. Wunderlich 1988).

The Salticidae is the largest extant spider family with more than 4800 species in 531 genera (Platnick 2002) and has a worldwide distribution. They occur frequently as Tertiary fossils, for example in ambers from the Baltic region (e.g. Petrunkevitch 1958) and the Dominican Republic (e.g. Wunderlich 1988). However, no salticids have been described from older strata, amber or otherwise (the specimen listed as a salticid in New Jersey amber by Grimaldi et al. (2002) is a misidentification, DP pers. obs. and the specimen figured as Salticidae by Néraudeau et al. (2002) from Cretaceous amber of France has not been described and does not clearly show the diagnostic features of the family), yet it is evident that many extant spider families have a long geological history (Selden & Penney 2001). The active predatory behavior of salticids, predisposes them to becoming trapped in resin (Penney 2002), so it may be that the Salticidae are a recently evolved family and that in earlier times their niche was occupied by a now extinct spider family such as the Lagonomegopidae or indeed, that the Salticidae may have evolved from the latter family (Eskov & Wunderlich 1994). In recent years, new Cretaceous material has become available which is currently being studied and will hopefully shed some light on this problem.

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WEB ORIENTATION OF THE BANDED GARDEN SPIDER *ARGIOPE TRIFASCIATA* (ARANEAE, ARANEIDAE) IN A CALIFORNIA COASTAL POPULATION

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ABSTRACT. Magnetic heading (direction the spider's ventrum faced) and web inclination (degree of slant from the vertical) in *Argiope trifasciata* Forskål, a diurnal orb-weaving spider, were studied at a coastal site in southern California for nine weeks in fall 1999. Throughout the study, *A. trifasciata* largely occupied east-west oriented webs with their venters facing south and southwest. Mean magnetic heading was unaffected by ambient temperature extremes. Inclination levels varied from week to week over an approximately 5° range. However, these changes followed no discernible pattern and were independent both of the sun's decrease in maximum altitude during the course of the study and of magnetic heading. Since the ventrum of *A. trifasciata* is dark, the consistent southern orientation exhibited by spiders at our study site suggests that they sought to maximize solar radiation in an attempt to gain heat. In addition, the east-west, facing-the-sun orientation of webs at this site places them parallel to the prevailing western breezes, minimizing their exposure to wind disturbance. As for inclination, it is unclear what factors may be influencing the degree of slant in *A. trifasciata* webs and further study will be needed to ascertain what they might be.

Keywords: Araneidae, *Argiope trifasciata*, web orientation, web inclination, solar radiation

For diurnal web building spiders which may occupy partially to fully exposed positions in their webs for long periods, thermal stress due to excessive heating by the sun or exposure to low temperature conditions could be a significant problem. Spiders from a variety of taxa have demonstrated web orientations which minimize or maximize insolation for the resident spiders. For example, Riechert & Tracy (1975) documented how the funnel webs of the desert agelenid *Agelenopsis aperta* (Gertsch 1934) are oriented to limit exposure to direct sunlight during the day. Biere & Uetz (1981) found that the orb webs of the forest araneid *Micrathena gracilis* (Walckenaer 1805) were oriented in a north-south plane (spiders facing east-west) in warm, well lit microhabitats, while webs in cool, shaded microhabitats had an east-west orientation (spi-

ders facing north-south). Such orientations would minimize the amount of body surface subject to insolation at midday for spiders in the well lit, warm microhabitats and would maximize the amount of body surface exposed to the sun's rays at midday for spiders in the shaded, cool microhabitats (Higgins & Ezcurra 1996). This method of modifying heat load via web directional orientation will be considered a form of thermoregulation in this paper. Spiders from a variety of taxa have also been shown to make deliberate postural adjustments while in their webs which act to reduce or increase their exposure to insolation (Pointing 1965; Krakauer 1972; Robinson & Robinson 1973, 1974, 1978; Tolbert 1979; Biere & Uetz 1981; Suter 1981; Higgins & Ezcurra 1996).

Web orientations interpreted as responses to conditions of high or low ambient temperatures and insolation have been reported for the large araneids *Argiope trifasciata* Forskål 1775 (Tolbert 1979) and *Nephila clavipes* (Linnaeus 1767) (Krakauer 1972; Carrel 1978; Higgins & Ezcurra 1996). However, in the case of *N. clavipes*, other studies have failed to find a relationship between web orientation

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and insolation (Robinson & Robinson 1974; Higgins & McGuinness 1991), suggesting regional variation in the use of web orientation as a thermoregulatory response in the Araneidae.

To explore this possibility further, this study examines whether the orb webs of *A. trifasciata* at a southern California locality might be oriented non-randomly with respect to solar radiation. As prior knowledge of web orientation in *A. trifasciata* is limited to two works conducted exclusively in temperate old field habitats east of the Mississippi (Coventry 1967; Tolbert 1979), we were interested in learning whether spiders at our Pacific coast study site would demonstrate any of the web orientation patterns seen in *A. trifasciata* (and other orb weaving taxa) elsewhere.

METHODS

Study species.—The banded garden spider, *A. trifasciata*, is abundant in the United States and its large orb webs are common in the vegetation of fields, gardens and roadsides (McNett & Rypstra 1997; Ramirez & Haakonsen 1999). *Argiope trifasciata* has an annual life-cycle; spiderlings emerge from overwintering eggsacs in spring and adults may be collected from summer to early fall (McReynolds & Polis 1987). Their web is a standard orb, composed of radii, sticky spirals, supporting frames, and sometimes stabilimenta (see Tso 1999 for a detailed description). The resident spider normally hangs head down from beneath the hub of the web, which is typically inclined slightly from the vertical (Tolbert 1975). In this paper, we will refer to the web face from which the spider hangs as the web underside (following Robinson & Robinson 1978) and the opposite face as the web upperside.

Study site.—The study population inhabited the undeveloped, elongate dune system at the western edge of the Ballona property adjacent to Playa del Rey, California, owned by Playa Capital Company, LLC. Located less than 0.5 km from the Pacific Ocean, the 372 m long dune system is bounded on the west by a linear series of apartment complexes sitting atop an approximately 3.7 m high berm, on the north by the Ballona Creek Channel, on the east by wetlands, and on the south by dirt roads (Schreiber 1981). We found webs primarily in coastal dune vegetation such as

bush lupine (*Lupinus arboreus*, *L. chamissonis*), as well as in wetlands pickleweed (*Salicornia subterminalis*, *S. virginica*) along the eastern dunes/wetlands boundary.

Web measurements.—The web sites of 124 large immature and adult female spiders were marked with numbered stake flags on Saturdays from 2 October—27 November 1999. The number present in any given week varied from 13–37. When initially discovered, resident spiders were removed from their webs and quickly transported to the laboratory. They were marked with dots of scale model paint along the periphery of the abdominal dorsum using a modification of the 1—2—4—7 numbering system of Brussard (1971), with each spider being marked to match its respective web site number. Marked spiders were returned to their webs as soon as possible, usually within 3 hr after capture. However, once the study was underway, we periodically discovered evidence of the partial loss of marker dots from some individuals, casting doubt on the reliability of field identification of individuals. In addition, our study site was vandalized and some marker flags were destroyed or moved. Consequently, this study focuses on changes in web orientations from week to week for the population as a whole, following Carrel (1978).

The web parameters measured were magnetic heading (the compass direction of the ventrum of the spider) and web inclination (degree of slant from the vertical). Magnetic headings were measured using a Suunto compass; the angle of orientation was that of a hypothetical dorsal-ventral line emerging from the spider's ventral side (as in Tolbert 1979), with reference to a north compass orientation of 0°. Inclination was determined using a protractor-plumb bob device; the straight edge of the protractor was placed parallel to and near the underside of the slanted web and the angle of the plumb bob string, reflecting the web's deviation from the vertical plane (angle = 0°), was recorded.

Data analysis.—For each week's magnetic heading values, we calculated the mean angle (α) and Rayleigh's r , a measure of the variance around the mean angle, and tested it for significance to determine if the data varied from a uniform circular distribution (Schmidt-Koenig 1975). Homogeneity among the weekly mean angles was analyzed using a multi-

sample Watson-Williams test (Rao & Sengupta, 2001). To see if the magnetic heading data might cluster around the sun's azimuth at sunrise, sunset or at noon, we conducted V-tests (Zar 1999) for each week's heading values using the sun's azimuth for each case (sunrise, sunset, noon). Azimuth data for the nine data collection dates (2 October–27 November) were obtained from the Astronomical Applications Department, U.S. Naval Observatory (<http://aa.usno.navy.mil/AA/data/>).

To determine if magnetic heading was affected by temperature changes over the nine week study, we generated regression plots of mean angle/week vs. the high and low temperatures for the Friday preceding each data collection. While orb-weavers normally build a new web daily (Carico 1986), *A. trifasciata* is not known to work on its web during daylight hours (Tso 1999), and so the webs we visited during our Saturday morning data collections were presumably mostly constructed overnight, perhaps influenced by the temperature conditions of the prior day. The temperature data used here are for Los Angeles International Airport (LAX) (located less than 3.0 km south of the study site), as listed in the weather section of the Los Angeles Times newspaper (<http://www.weatherpoint.com/latimes/>). Temperatures were unavailable for one Friday (5 November), so the regression analyses were based on data for the remaining eight weeks. While the airport is at a higher elevation (≈ 30 m) than the coastal plain which includes the Ballona study site (\approx sea level), long-term records indicate that October–November temperatures are virtually the same for both areas (Felton 1965).

Inclination data have been summarized via weekly means. To determine if these data exhibited any trend during the course of the study, we performed linear regression of mean inclination/week vs. week. In addition, to ascertain if inclination is influenced by the sun's changing position over time (as implied by Moore 1977), we regressed mean inclination/week against the sun's maximum altitude (angle from the horizon). Altitude data for the nine sample days (2 October–27 November) were obtained from the Astronomical Applications Department, U.S. Naval Observatory (<http://aa.usno.navy.mil/AA/data/>). Finally, to determine if inclination is related to magnetic

Table 1.—Magnetic heading and web inclination data for *Argiope trifasciata* at Ballona October–November 1999. Sampling dates are in day/month shorthand format. Magnetic heading is with reference to the ventral surface of spiders sitting on webs. Angle refers to degree of slant of the plane of the web from the vertical plane (angle = 0°). Abbreviations: *n* = sample size; α = mean angle (vector); *r* = a measure of the variance around the mean angle, used in the Rayleigh test for unimodality in a sample, for which the respective *P* values are indicated. ** *P* < 0.01; *** *P* < 0.001.

Date	Magnetic Heading			Inclination	
	<i>n</i>	α	<i>r</i>	<i>n</i>	Angle (°)
2 Oct	11	235.73°	0.792***	13	17.54
9 Oct	24	186.53°	0.499**	26	18.73
16 Oct	32	182.60°	0.666***	32	14.59
23 Oct	37	179.93°	0.635***	37	19.84
30 Oct	36	183.48°	0.733***	34	16.82
6 Nov	36	182.91°	0.572***	37	15.08
13 Nov	30	185.81°	0.703***	33	17.70
20 Nov	33	189.90°	0.709***	34	15.12
27 Nov	18	212.67°	0.698***	19	15.95

heading (e.g. Bishop & Connolly 1992), we generated regression plots of inclination vs. magnetic heading using only spiders for which both inclination and heading data were available. These analyses were performed separately by week, as well as for all data combined.

RESULTS

Magnetic heading.—According to the Rayleigh tests, all the samples are non-randomly distributed and all are significantly (*P*'s < 0.001) concentrated toward the S and SW (Table 1). The mean angle varied from 179.93°–235.73°, though for the middle seven weeks (9 October–20 November), it varied over a much smaller range (179.93°–189.90°). However, differences among these samples were non-significant (Watson-Williams test, *P* > 0.05). Hence, throughout this study, *A. trifasciata* occupied east-west oriented webs with the uppersides of webs and venters facing south and southwest.

Solar azimuths and magnetic heading: With all nine samples, the solar azimuths at noon (due south) and sunset (southwest) were both highly consistent with the observed magnetic headings (*P*'s < 0.001), based on the *V*-test

Table 2.—Results of *V*-tests for significant clustering of magnetic heading with respect to the azimuth of the sun at sunrise, noon and sunset. The date format follows Table 1. *Abbreviations:* *n* = sample size; α = mean angle (vector), reproduced from Table 1 for comparison with azimuth values; AZ = azimuth; *u* = *V*-test *u* statistic, for which the respective *P* values are indicated. *** *P* < 0.001.

Date	<i>n</i>	α	Sunrise		Noon		Sunset	
			AZ	<i>u</i>	AZ	<i>u</i>	AZ	<i>u</i>
2 Oct	11	235.73°	93.9°	−16.063	180.0°	11.506***	265.8°	17.682***
9 Oct	24	186.53°	97.3°	0.556	180.0°	41.217***	262.6°	9.989***
16 Oct	32	182.60°	100.4°	11.576***	180.0°	85.162***	259.5°	19.316***
23 Oct	37	179.93°	103.5°	23.719***	180.0°	101.054***	256.3°	23.805***
30 Oct	36	183.48°	106.4°	25.033***	180.0°	111.746***	253.5°	38.251***
6 Nov	36	182.91°	109.0°	24.218***	180.0°	87.255***	250.9°	32.738***
13 Nov	30	185.81°	111.5°	22.093***	180.0°	81.261***	248.3°	37.724***
20 Nov	33	189.90°	113.7°	22.668***	180.0°	93.621***	246.2°	57.732***
27 Nov	18	212.67°	115.4°	−4.771	180.0°	31.729***	244.5°	32.026***

results (Table 2). In addition, while the data failed to show significant orientation toward the sunrise azimuth (southeast) on three dates (2 October, 9 October, 27 November), significant orientations were detected on the other six dates (16 October—20 November) (*P*'s < 0.001).

Multiple *V*-tests using a single circular data set and several predicted directions will sometimes indicate consistency with more than one direction, though in such cases, inspection of the magnitude of the *V*-test *u* statistics will indicate which direction is most compatible with the particular data set (examples in Gould & Gould 2002). With *A. trifasciata*, such an approach clearly indicates greatest compatibility with the noon azimuth (due south) for the middle seven weeks (9 October—20 November), as the values of *u* for this azimuth are typically two to four times greater than those for the sunrise and sunset azimuths during this period (Table 2). With the two remaining dates (2 October, 27 November), the *u* values for the sunset azimuth (southwest) are numerically larger than those for the noon azimuth (though only slightly for 27 November), indicating greater compatibility with the heading data. As the mean angles (α 's) for these dates (235.73°, 212.67°, respectively) are more southwesterly than values for any other date (all < 190°), the *V*-test results for these dates are not unexpected. Overall, the *V*-test analyses underscore *A. trifasciata*'s preference for web placement at Ballona with the upper-sides facing south and southwest.

Temperature and magnetic heading: While

Friday temperatures varied widely during the nine weeks of this study (highs: 19.4–31.3 °C; lows: 10–16.1 °C), no significant relationship exists between magnetic heading and either highs (r^2 < 0.0005, *P* = 0.958) or lows (r^2 = 0.003, *P* = 0.895). Magnetic heading at our study site was therefore unaffected by the temperature extremes of the prior day.

Inclination.—Mean inclination values varied randomly from week to week during this study and did not display any trend with time (Table 1; r^2 = 0.161, *P* = 0.284).

Solar altitude and inclination: Analysis of mean inclination values plotted against the sun's maximum altitude for each sample date yields a positive slope (0.116), but this relationship is non-significant (*P* = 0.292), indicating that web placement in the vertical plane was independent of the sun's change in altitude during the course of this study.

Magnetic heading and inclination: No relationship was found between inclination and magnetic heading. This was true for both the nine weekly samples considered individually (r^2 's = 0.0004–0.124, *P*'s = 0.151–0.910), as well as for all data combined (r^2 = 0.002, *P* = 0.471). Hence, the inclination of a web was not influenced by its directional orientation.

DISCUSSION

Magnetic heading.—Our magnetic heading findings for *A. trifasciata* differ somewhat from those of prior investigations. Based on a June–October study of a population in an old field habitat in Tennessee, Tolbert (1979) found that magnetic heading was random for

2/3 of all observations, with significant directionality being seen on selected dates only during the hottest (August) and coldest (October) months. Random magnetic headings during summer (July) have also been described for *A. argentata* (Fabricius) in open grassy areas in Panama (Robinson & Robinson 1978). During Tolbert's (1979) August observations, spiders largely occupied east-west oriented webs with their silver/white dorsums facing south and their dark ventrums facing north, while during October, the situation was reversed, with the dorsums facing north and the ventrums facing south as spiders occupied east-west webs. Having the reflective dorsum facing the sun was interpreted as a means of lowering body temperature, while having the dark ventrum facing the sun was thought to be a means of increasing body temperature (Tolbert 1979). Coventry (1967) (as cited by Tolbert 1979) reported similar findings for a population of *A. trifasciata* in Wisconsin.

In contrast, magnetic headings of *A. trifasciata* at our coastal study site were never random and web placement was such that web uppersides and bodily venters generally faced the sun. The fact that spiders in our study never displayed the significant web underside/dorsum-facing-the-sun pattern described by Tolbert (1979) during hot periods, even on dates following Fridays with high ambient temperatures, suggests that dealing with a high heat load was not a significant problem. Rather, the consistent, ventrum-facing-the-sun directionality exhibited by spiders at our study site suggests that staying warm is the greater challenge. In this regard, it should be noted that this solar directionality was usually achieved by facing the plane of the web toward the sun at its noontime and sunset positions (due south; southwest), rather than toward the direction of its rising (southeast), the preferred heading in studies of two other araneids [*N. clavipes* (Carrel 1978); *Mangora gibberosa* (Hentz, 1847) (Caine & Hiebert 1987)]. This may be an adaptation to the generally overcast conditions which prevail at the Ballona study site during the morning hours (see below), which may significantly obscure the sun till it has progressed far beyond its sunrise azimuth.

We hypothesize that coastal *A. trifasciata* may seek to maximize bodily exposure to the sun in response to the cooling effects of cloud

cover and fog which typify the coastal zone (Maritime Fringe) in southern California from late afternoon until potentially noon the following morning (Bailey 1966; Schoenherr 1992). These cloud/fog layers reduce daytime solar radiation by reflecting or absorbing much of the incoming light energy and collectively truncate the number of daytime hours with unobstructed sunlight (Holland & Keil 1995). Even during the heat of the day after clouds and fog "burn off", the actual body temperatures of diurnal orb weavers at our study site may be lowered by convective heat exchange resulting from the fairly constant onshore flow of marine air which characterizes coastal Los Angeles (Bailey 1966; Schoenherr 1992).

Of course, it is also possible that magnetic heading at our study site had less to do with thermal considerations and more to do with factors such as habitat characteristics, exposure to potential predators, and prey sources, which have all been shown to influence web siting and form (Janetos 1986; Riechert & Gillespie 1986; Wise 1993). For example, large *Metepeira datona* Chamberlin & Ivie 1942 on a small Bahamian island oriented the plane of their orbs parallel to the prevailing wind, presumably to minimize wind damage (Schoener & Toft 1983). This may also be the case with *A. trifasciata* webs at Ballona, as their generally east-west planar orientation would indeed be mostly parallel to the western breezes accompanying the onshore flow. Moreover, as the radial threads in an orb web can be plasticized by contact with water (Vollrath & Edmonds 1989), potentially diminishing their ability to support both prey and the resident spider, such a facing-the-sun orientation may also facilitate the evaporation of web-borne dew/rain drops and the drying out of radial threads. Clearly, a comprehensive study involving longer-term monitoring of magnetic heading and other biotic/abiotic variables in both coastal and inland populations of *A. trifasciata* in southern California will be needed to fully assess the generality and significance of the presumed "insolation seeking" heading displayed by our Ballona population.

Inclination.—The webs of most araneids make at least a small angle with the vertical (Eberhard 1972), such that the spider's own weight pulls it away from the web's underside, which likely facilitates moving about the web

while avoiding sticky spirals (Peters 1932). What other purposes may be served by *A. trifasciata* having an inclined web is unclear in light of the present results, as well as prior studies.

Krakauer (1972) suggested inclination may have a thermoregulatory role, noting that the slight angle of *N. clavipes* webs in Florida decreases the angle through which the tip of the abdomen has to swing in order to be pointing directly toward the sun on warm days, thereby minimizing the body surface exposed to insolation. This would imply that webs which are less vertical (more inclined) may be associated with the greater insolation of summer and webs which are more vertical (less inclined) with the lower insolation of fall/winter, as a response to decreased solar heating accompanying this seasonal transition. However, Moore's (1977) May–November field study of *N. clavipes* in Texas found exactly the opposite trend, an increase in inclination over time. With *A. trifasciata* at Ballona, inclination did not exhibit either a decreasing or increasing trend and showed no relationship to the decrease in the sun's maximum altitude during the study period, suggesting no interaction between thermal factors and inclination. However, as we did not quantify posturing behavior, we can not conclusively rule out a thermoregulatory role for inclination at this time.

Eberhard (1971) proposed that the degree of inclination may be a response to wind speed, having found that orb webs of *Uloborus diversus* Marx 1898 in Arizona exposed to prevailing winds were more horizontal than webs in protected sites, presumably to minimize damage from horizontal winds. While this finding would suggest that the degree of inclination might be related to wind direction for spiders in an open setting like Ballona, the inclination of *A. trifasciata* webs was unrelated to their magnetic heading. Bishop & Connolly (1992) also found no relationship between inclination and magnetic heading for the tropical orb weaver *Leucage regnyi* (Simon 1877) in Puerto Rico. Obviously, further study of inclination and other biotic/abiotic variables in both coastal and inland populations will be needed to elucidate the factors influencing web slant in *A. trifasciata*.

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THE FIRST DNA PHYLOGENY OF FOUR SPECIES OF *MESOBUTHUS* (SCORPIONES, BUTHIDAE) FROM EURASIA

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ABSTRACT. The first molecular phylogeny is presented for four species of the scorpion genus *Mesobuthus*, based on DNA sequences of three gene fragments (two mitochondrial and one nuclear protein coding gene, ~1 kb). The inferred phylogeny based on a pooled maximum likelihood analysis revealed a clear deep splitting between the “western clade” consisting of *M. gibbosus* and *M. cyprius* (Greece/Anatolia, Cyprus) and the “eastern clade” consisting of *M. eupeus* and *M. caucasicus* (Anatolia/Central Asia). The species *M. caucasicus* (recently placed in the genus *Olivierus* Farzanpay 1987) groups monophyletically within *Mesobuthus*; thus, the genus *Olivierus* is synonymized here with *Mesobuthus*. Sequences of *M. eupeus* and *M. caucasicus* sampled mainly from Kazakhstan and Uzbekistan are highly structured, indicating the possible existence of multiple species.

Keywords: Scorpions, Buthidae, *Mesobuthus*, phylogeny, DNA, 16S, *cox1*, protein kinase, biogeography

The genus *Mesobuthus* Vachon 1950 (Scorpiones, Buthidae) currently includes 12 species (Fet & Lowe 2000; Gantenbein et al. 2000b); its type species is *Mesobuthus eupeus* (C.L. Koch 1839). Except for *M. gibbosus* (Brullé 1832), which is found in the Balkans and Turkey, the diversity of this genus is concentrated in Asia. Numerous species and subspecies are distributed from Turkey to Korea, with the centers of diversity in Central Asia and Iran. *Mesobuthus* species are the most common and abundant scorpions in a variety of arid habitats, from sand deserts to high mountains over 3000 m (Fet 1989, 1994). They are found up to 50°N in Kazakhstan, the northern limit of the natural range of the Old World scorpions (Gromov 2001).

Although Buthidae are the most diverse and medically important family of scorpions (Fet & Lowe 2000), there has been no attempt so far to produce a phylogenetic analysis of this family. Especially powerful are phylogenies based on DNA sequence data in combination with morphology (Gantenbein et al. 1999a, 2000a; Fet et al. 2001). Our first applications of this technique in Buthidae refer to the gen-

era *Buthus* Leach 1815 (Gantenbein et al. 1999b; Gantenbein & Lariadèr 2003) and *Centruroides* Marx 1890 (Gantenbein et al. 2001; Towler et al. 2001); we also published a pilot phylogeny of 17 buthid genera (Fet et al. 2003). Molecular markers helped to define island species, where neither the biological species concept nor any other species concept can be applied (Gantenbein et al. 2000b, 2001).

METHODS

The currently studied available material belonged to four species: *Mesobuthus gibbosus* (Greece, Turkey), *M. cyprius* Gantenbein & Kropf 2000 (Cyprus), *M. eupeus* (C.L. Koch 1839) (Turkey, Kazakhstan, Turkmenistan, Uzbekistan, China), and *M. caucasicus* (Nordmann 1840) (Kazakhstan, Turkmenistan, Uzbekistan) (see Table 1 for locality information). For DNA analyses, the total DNA was extracted from fresh or preserved (94–98% ethanol) muscle tissue using a standard phenol/chloroform and precipitation method (Sambrook et al. 1989). We amplified a ca. 450 base pair (bp) fragment of the 16S rRNA mitochondrial (mt) DNA by polymerase chain reaction (PCR) using the primers and condi-

Table 1.—Sampling sites and country of origin of *Mesobuthus* species used in this study.

Abbreviation	Country	Locality	Coll.	EMBL accession nos.		
				16S	coxI	PK
<i>M. caucasicus</i> (Nordmann 1840)						
<i>McaKZa1</i>	Kazakhstan	Kapchagai	Ch. Tarabaev, 1990	AJ550674	AJ550692	AJ550713
<i>McaKZb1</i>	Kazakhstan	Baigakum	V. Fet & A. Gromov, 25-V-2002	AJ550675	AJ550693	AJ550714
<i>McaUZa1</i>	Uzbekistan	Bukhara	V. Fet & A. Gromov, 20-IV-2002	AJ550676	AJ550694	AJ550715
<i>McaUZb1</i>	Uzbekistan	Jarkurgan	V. Fet & A. Gromov, 26-IV-2002	AJ550677	AJ550695	AJ550716
<i>McaUZc1</i>	Uzbekistan	Karakalpak Steppe, Fergana	V. Fet & A. Gromov, 20-V-2002	AJ550678	AJ550696	AJ550717
<i>McaUZd1</i>	Uzbekistan	Babatag Mountains	V. Fet & A. Gromov, 30-IV-2002	AJ550679	AJ550697	AJ550718
<i>M. cyprius</i> Gantenbein & Kropf 2000						
<i>McyCYa1</i>	Cyprus	Tepebasi	A. Scholl, 27-IX-1997	AJ550680	AJ550698	AJ550719
<i>McyCYb1</i>	Cyprus	Kantara	A. Scholl, 20-V-1998	AJ550681	AJ550699	AJ550720
<i>M. eupeus mongolicus</i> (Birula 1911)						
<i>MeuGobi1</i>	China	Gobi Desert	A. Davidson, 30-VII-1998	AJ550682	AJ550700	AJ550721
<i>M. eupeus eupeus</i> (C.L. Koch 1839)						
<i>MeuTRA1</i>	Turkey	Gölsehir, Central Anatolia	A. Scholl, 28-V-1998	AJ550688	AJ550701	AJ550722
<i>MeuTRb1-2</i>	Turkey	Cemilköy, Central Anatolia	A. Scholl, 31-V-1998	AJ550689–90	AJ550702–03	AJ550723–24
<i>M. eupeus thersites</i> (C.L. Koch 1839)						
<i>MeuKZa1</i>	Kazakhstan	Bakanas	A. Gromov, 2-5-VI-2000	AY228141	AJ550704	AJ550725
<i>MeuKZb1</i>	Kazakhstan	Baigakum	V. Fet & A. Gromov, 23-V-2002	AJ550684	AJ550705	AJ550726
<i>MeuKZc2</i>	Kazakhstan	Karatau Mountains	V. Fet & A. Gromov, 27-V-2002	AJ550685	AJ550706	AJ550727
<i>MeuTU1a</i>	Turkmenistan	Repetek, Karakum	V. Fet & A. Gromov, 15-18-IV-2002	AJ550686	AJ550707	AJ550728
<i>MeuUZa1</i>	Uzbekistan	Zarafshan, Kizylkum	A. Gromov, 18-IV-1998	AJ550687	AJ550708	AJ550729

Table 1.—Continued.

Abbreviation	Country	Locality	Coll.	EMBL accession nos.		
				16S	coxI	PK
<i>MeuUZb1</i>	Uzbekistan	Babatag Mountains	V. Fet & A. Gromov, 29-IV-2002	AJ550683	AJ550709	AJ550730
<i>Mesobuthus gibbosus</i> (Brullé 1832)						
<i>MgiGRa1</i>	Greece	Mathia, Peloponnesos	I. & B. Gantenbein, 18-III-1998	AJ402571	AJ550710	AJ550731
<i>MgiGRb1</i>	Greece	Igoumenitsa, Epirus	I. & B. Gantenbein, 28-IV-1998	AJ550691	AJ550711	AJ550732
<i>MgiTRa1</i>	Turkey	Avanos, Central Anatolia	A. Scholl, 28-V-1998	AJ402587	AJ550712	AJ550733
Outgroup: <i>Androctonus australis</i> (Linnaeus 1758)						
<i>AanTNa1</i>	Tunisia	Nefta	A. Scholl, 27-IV-1999	AJ506868	AJ506919	AJ550734

tions of Gantenbein et al. (1999). For the partial amplification of the cytochrome oxidase I (*coxI*) gene we used the primers *LCO* (Folmer et al. 1994) and *Nancy* (Simon et al. 1994) which amplify a ~850 bp fragment (positions ~30–850 of the *Drosophila yakuba* sequence; Flybase: FBgn0013179). We used the following PCR profile: initial denaturation 94 °C for 4 min followed by 40 cycles of 25 s at 94 °C, 20 s at 51 °C, and 90 s at 72 °C. In addition, we designed new buthid-specific PCR primers from a clone (03B09) of an EST library of *Mesobuthus gibbosus* (unpublished data, Gantenbein et al., in preparation) to amplify a ~360 bp fragment of the nuclear protein kinase (PK) gene (Flybase locus CG11221, identified from BLASTX against the *Drosophila* protein database, similarity 43%, Expectation = 5e–14). The primers were *03B09for* 5'-TCT GAT GTA TGG CAG ATG GCA ATG-3' and *03B09rev* 5'-CGA ACT

CAA GAT CCA CTC CTG TAC TCG-3'. We used the same PCR profile as for *coxI*. PCR primers were removed by polyethylene glycol (PEG 8000) precipitation, and templates were directly sequenced on one strand using one of the PCR primers and DYEnamic ET Dye Terminator Kit (Amersham Biosciences). For *coxI* and PK we used the forward PCR-primers for sequencing, and for the 16S we used the same primer as in Gantenbein et al. (1999). Sequencing reactions were ethanol/sodium-acetate precipitated and run on an ABI377XL sequencer (Applied Biosystems, Foster City, CA). All sequences were checked manually for sequencing errors. All sequences were deposited in the EMBL nucleotide sequence database (<http://www.ebi.ac.uk>). As outgroup, we used the Old World buthid *Androctonus australis* (L. 1758) from Nefta, Tunisia (AauTNa1), which is a suitable outgroup for the genus *Mesobuthus* as indicated from

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Figure 1.—Maximum Likelihood (ML) tree of *Mesobuthus* species from southern Europe, Western and Central Asia inferred from three combined DNA sequence fragments of the mitochondrial 16S, *coxI* and the nuclear PK regions, 1,095 bp (–ln Likelihood was 5505.86). The DNA substitution model was TRN + Γ + I (Tamura & Nei 1993); base frequencies: $\pi_A = 0.29$, $\pi_T = 0.37$, $\pi_C = 0.14$, $R_{matrix} = (A-G = 6.70, A-C = A-T = G-T = 1, C-T = 3.56)$, gamma shape parameter $\alpha = 0.53$, and proportion of invariable sites = 0.37, respectively. The tree was rooted using the outgroup species *Androctonus australis* (AauTNa1). Numbers at nodes refer to bootstrap support given as percentage from 1,000 pseudo replicates by neighbour-joining of ML distances.

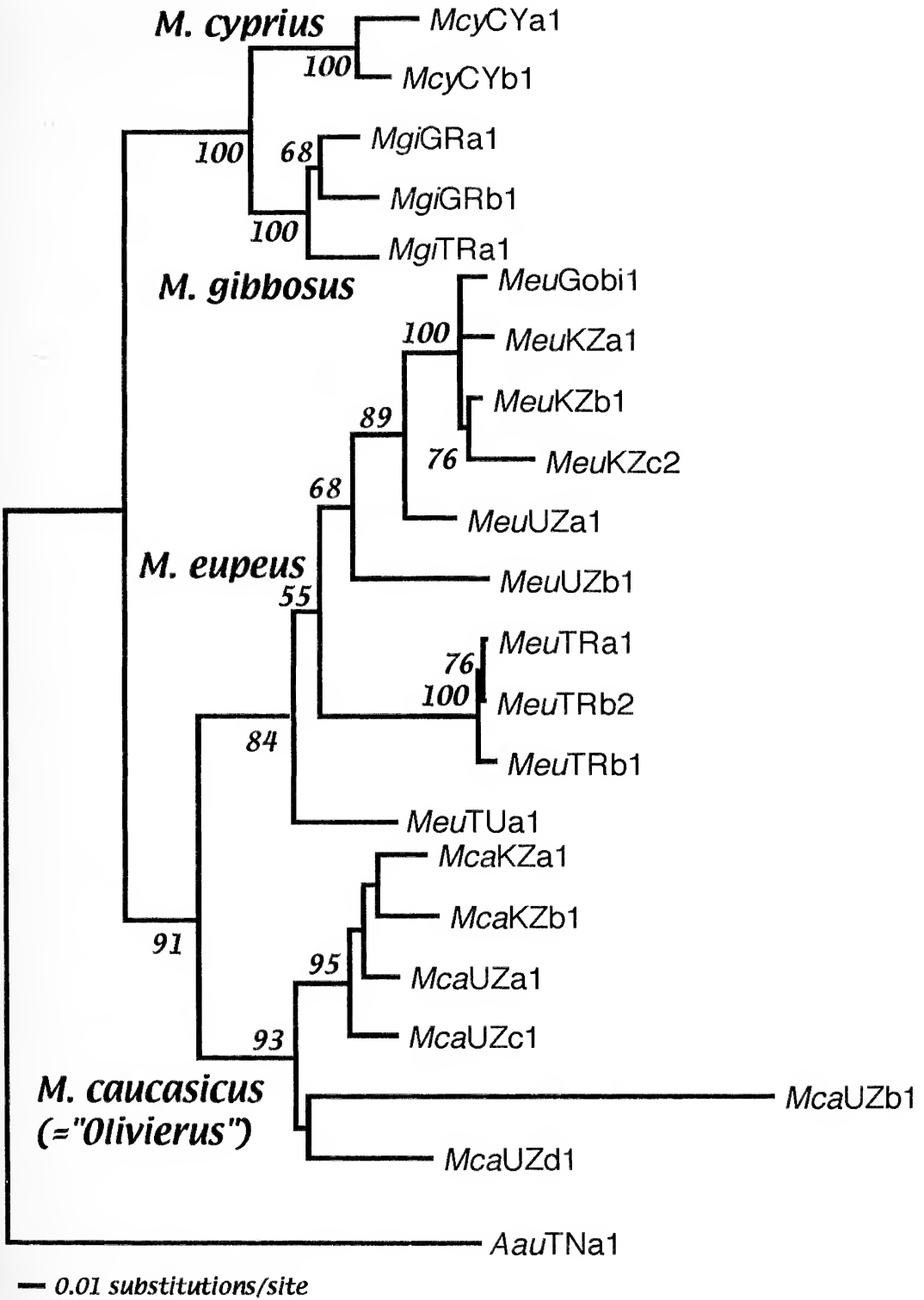


Table 2.—Estimates of average rates of synonymous substitutions (K_S) (lower left) and non-synonymous (K_A) (upper right) substitution per site among four species of *Mesobuthus* of two protein-coding gene fragments. Diagonals show average K_S and K_A (in parentheses) among haplotypes within species. Estimates of nucleotide diversity π for each species (Nei & Li 1979) are given in the last column.

	<i>cyprius</i>	<i>caucasicus</i>	<i>eupeus</i>	<i>gibbosus</i>	diversity π
coxI locus					
<i>cyprius</i>	0.11 (0.009)	0.297	0.024	0.006	0.037
<i>caucasicus</i>	0.844	0.482 (0.030)	0.034	0.023	0.098
<i>eupeus</i>	0.887	0.753	0.377 (0.026)	0.023	0.089
<i>gibbosus</i>	0.538	0.892	0.692	0.223 (0.004)	0.048
PK locus					
<i>cyprius</i>	0.038 (0.018)	0.106	0.013	0.013	0.032
<i>caucasicus</i>	0.093	0.022 (0.000)	0.004	0.004	0.008
<i>eupeus</i>	0.073	0.032	0.008 (0.000)	0.009	0.002
<i>gibbosus</i>	0.04	0.082	0.064	0.037 (0.009)	0.017

morphology (Vachon 1952). Voucher specimens will be deposited in the Natural History Museum, Bern, Switzerland (NHMBE).

The resulting 22 16S DNA sequences were aligned using ClustalX (Thompson et al. 1997) and by eye. We applied Maximum Likelihood (ML) to the DNA sequence data. The alignment was 344 bp long. The alignment was deposited in the EMBL nucleotide database (ALIGN_000522). Ambiguities and gaps were stripped out (Swofford et al. 1996), leaving 302 bp. The alignment of the *coxI* and the PK fragments was unambiguous because of the open reading frames (ORF). In order to choose the most appropriate DNA model of nucleotide substitution, we calculated hierarchical likelihood ratio test statistics using MODELTEST 3.06 (Posada & Crandall 1998; Huelsenbeck & Rannala 1997) which is implemented in PAUP* 4.0b10 (Swofford 1998) and calculates the hierarchical likelihood ratio statistics (LRT) of 56 different substitution models based on a NJ tree using JC69 distances (Jukes & Cantor 1969). The rate heterogeneity among sites was assumed to follow a gamma distribution (shape parameter α was ML-estimated) with four categories, each represented by its mean (Yang 1996). The ML-estimated parameters and the model are given in the legend of Fig. 1.

The tree topology found with ML of the pooled mitochondrial data (16S & *coxI*) was not significantly different from the topology inferred from the nuclear PK gene if assessed by the two-tailed K-H-test ($-\ln L_{(\text{tree PK|PKdata})} = 618.49$; $-\ln L_{(\text{tree 16S\&coxI|PKdata})} = 632.50$; $P =$

0.16) with re-estimation of maximum likelihood by non-parametric bootstrapping (RELL) (Kishino & Hasegawa 1989; Kishino et al. 1990). Thus, we pooled the nuclear and mitochondrial data, leaving 1,095 bp (475 bp of the *coxI* and 318 bp of the PK, excluding gaps and ambiguities).

In a further step, the molecular clock hypothesis (i.e., equal rates across all sequences) was tested using the χ^2 approximated likelihood ratio test statistics with OTU's-2 degrees of freedom ($df = 22-2 = 20$) which was rejected with a P -value < 0.01 (Huelsenbeck & Crandall 1997). We explored the tree space by 100 heuristic tree searches using the Tree-Bisection-Reconnection (TBR) algorithm and by randomizing the order of the sequence input in PAUP*. Phylogenetic trees were rooted using *Androctonus australis* as an outgroup. Statistical confidence of phylogenies was assessed using the bootstrap procedure (1,000 pseudoreplicates) (Felsenstein 1985) using PAUP*. These distances were usually $\sim 15\%$ between *Mesobuthus* species and go up to $\sim 20\%$ if *Mesobuthus* sequences were compared to the outgroup.

RESULTS AND DISCUSSION

The three analyzed DNA fragments contained considerable polymorphism among but also within species as estimated using Nei & Li's (1979) nucleotide diversity π and the amount of synonymous versus non-synonymous substitutions of coding regions (Jukes & Cantor 1967) (Table 2). We found 153 mutations out of 475 bp (of which 29 were replace-

ment changes) in the *coxI* fragment, and 19 mutations out of 318 bp (of which 8 were replacement changes) in the PK gene (excluding the outgroup). The 16S fragment contained 131 polymorphic sites out of 302 bp.

The recovered phylogeny (Fig. 1) showed high support for all four included species. This phylogeny allows to address several important taxonomic and evolutionary issues pertaining to the genus *Mesobuthus*. First of all, the phylogeny demonstrates a deep split between the “western clade” of *M. gibbosus* and *M. cyprius* and the “eastern clade” of *M. eupeus* and *M. caucasicus* (Fig. 1); each clade is well supported (100% and 92% bootstrap, respectively). Within the “eastern clade,” there is a strong support for currently accepted species *M. eupeus* (87%) and *M. caucasicus* (94%). The *Mesobuthus caucasicus* sequences are nested within the genus *Mesobuthus* as a sister group to *M. eupeus*. This observation is important as the generic placement of *M. caucasicus* has been controversial since Farzanpay (1987) created a separate monotypic genus *Olivierus* for this species. As our molecular data show, this new genus is paraphyletic with respect to *Mesobuthus* (Fig. 1). Fet & Lowe (2000) listed *Olivierus* as a valid genus but noticed that it was created without any solid justification or revision. The only characters (number of granules on movable finger of pedipalp chela) that Farzanpay (1987) briefly quoted (in Farsi) in support of *Olivierus*, were borrowed from Vachon (1958) species-level descriptions, and are not diagnostic for a genus. Further, our molecular data do not support monophyly of *Olivierus*. Therefore, we propose to list this genus as a synonym of *Mesobuthus*, as was traditionally accepted by all authors before Farzanpay (1987): *Olivierus* Farzanpay 1987 = *Mesobuthus* Vachon 1950, NEW SYNONYMY.

Another observation refers to the subspecific structure of *M. eupeus*, the type species of the genus *Mesobuthus*. This species is extremely polymorphic, and has 14 formally valid subspecies ranging from Turkey to China (Vachon 1958; Fet 1989; Fet & Lowe 2000), with most subspecies described from Iran. The nominotypic subspecies *M. e. eupeus* (C.L. Koch 1839) is found in the Caucasus and Turkey, while most populations from Central Asia are classified as *M. e. thersites* (C.L. Koch, 1839). In our analysis, the nominotypic

subspecies (Turkey) is highly supported (bootstrap 100%) while the Central Asian sequences present a more complicated case. A separate clade exists for a sand desert population from Turkmenistan (MeuTUa1), as opposed to the clade of several populations from Uzbekistan, Kazakhstan and China (bootstrap 68%). This can be an indication of an ancient separation between southern and northern desert forms, possibly valid at least at the subspecies level (Fet 1994). The further phylogenetic analysis could result in elevating these subspecies to the species level. It is interesting that already Birula (1917) grouped all subspecies of *M. eupeus* into two species groups (“sections”), “*eupeus*” and “*thersites*”; however, status of these groups was never examined.

Within *M. caucasicus*, a very strongly supported clade (bootstrap 98%) groups populations from central Uzbekistan (Bukhara, Fergana) and Kazakhstan, while those from southern Uzbekistan (Jarkurgan, Babatag) group outside. It remains to be seen if genetic separation in this case is matched by the morphological variation, as there are several subspecies described from Central Asia as well.

In addition, in our phylogeny the northern Central Asian populations of both *Mesobuthus eupeus* and *M. caucasicus* (Kazakhstan) appear to be derived compared to the southern populations of both species (Uzbekistan); this could be the result of progressive Tertiary aridization and spreading of the arid scorpion species from south to north to the sand and clay deserts (Fet 1994).

The presented data also allow a calibration of a molecular clock using the separation of Cyprus from the Anatolian mainland (5.2 Mya) after the Messinian salinity crisis, during which gene flow between island and mainland populations could have been possible. The Mediterranean Basin was refilled within only 100 yrs, which provides an excellent calibration point for a molecular clock (Hsü et al. 1977; Gantenbein & Largiadèr 2002). Thus, the sequence divergence between Anatolia and Cyprus was estimated to 0.09 ± 0.01 (0.10 ± 0.01 for 16S), which results in a sequence divergence rate of 0.017 per My. This rate estimate is somewhat higher than previous estimates in scorpions for *Mesobuthus gibbosus* (Gantenbein & Largiadèr 2002) but lies absolutely in the range of scorpions such

as *Buthus occitanus* and *Centruroides* (Buthidae) and other invertebrates such as butterflies, beetles and crickets (Brower 1994; Fleischer et al. 1998; Gómez-Zurita et al. 2000; Gantenbein et al. 2001; Gantenbein & Lariadèr 2003).

The genus *Mesobuthus* was created when Vachon (1950) initiated a large-scale "splitting" revision of the traditional genus *Buthus* Leach 1815. Its composition is still controversial. For instance, several Indian species are classified currently in this *Mesobuthus* but their generic identity is unclear (Fet & Lowe 2000). Separate species have been only recently described from Cyprus (Gantenbein et al. 2000b) and confirmed for northern Israel (Fet et al. 2000). Numerous subspecies exist in *M. eupeus* and *M. caucasicus* but morphological characters are inconclusive as for their relationship and taxonomic status. Further application of new molecular markers will facilitate our understanding of taxonomy and evolution of this common scorpion genus.

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SHORT COMMUNICATION

CREEP AND LOW STRENGTH OF SPIDER DRAGLINE SUBJECTED TO CONSTANT LOADS

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ABSTRACT. Major ampullate (dragline) silk is attracting significant attention as a potentially useful engineering fiber. This interest is motivated by reports that the silk exhibits high mean strength, stiffness and toughness as measured in tensile tests. However, the typical testing conditions (constant strain rate; experiment completed within less than an hour) imposed during such assessments do not reflect typical demands (e.g. ability to support constant load for long times) made on real high-tensile materials. We demonstrate here that *Nephila clavipes* major ampullate silk subjected to constant loads performs poorly: its breaking strength is significantly lower than that measured in conventional constant strain rate tests, and even very small constant loads can cause elongation to increase appreciably over long timescales.

Keywords: Creep, dragline, *Nephila clavipes*, silk, strength

There is much current interest in major ampullate (dragline) silk, inspired by its headline strength, stiffness and toughness (Viney 2000b; Lazaris et al. 2002; Kubik 2002). Attempts are being made to produce economic quantities of silk-like protein in genetically altered organisms (Scheller et al. 2001; Lazaris et al. 2002), for spinning into high performance fibers. However, a functional engineering material must maintain its dependable properties, in an appropriate environment, for a serviceable period of time. The long-term tensile durability of spider silks has received scant evaluation. In this communication, we demonstrate that silk can undergo creep and catastrophic failure under ambient conditions, at stresses far lower than those needed to cause yield or fracture in a conventional (constant strain rate) tensile test.

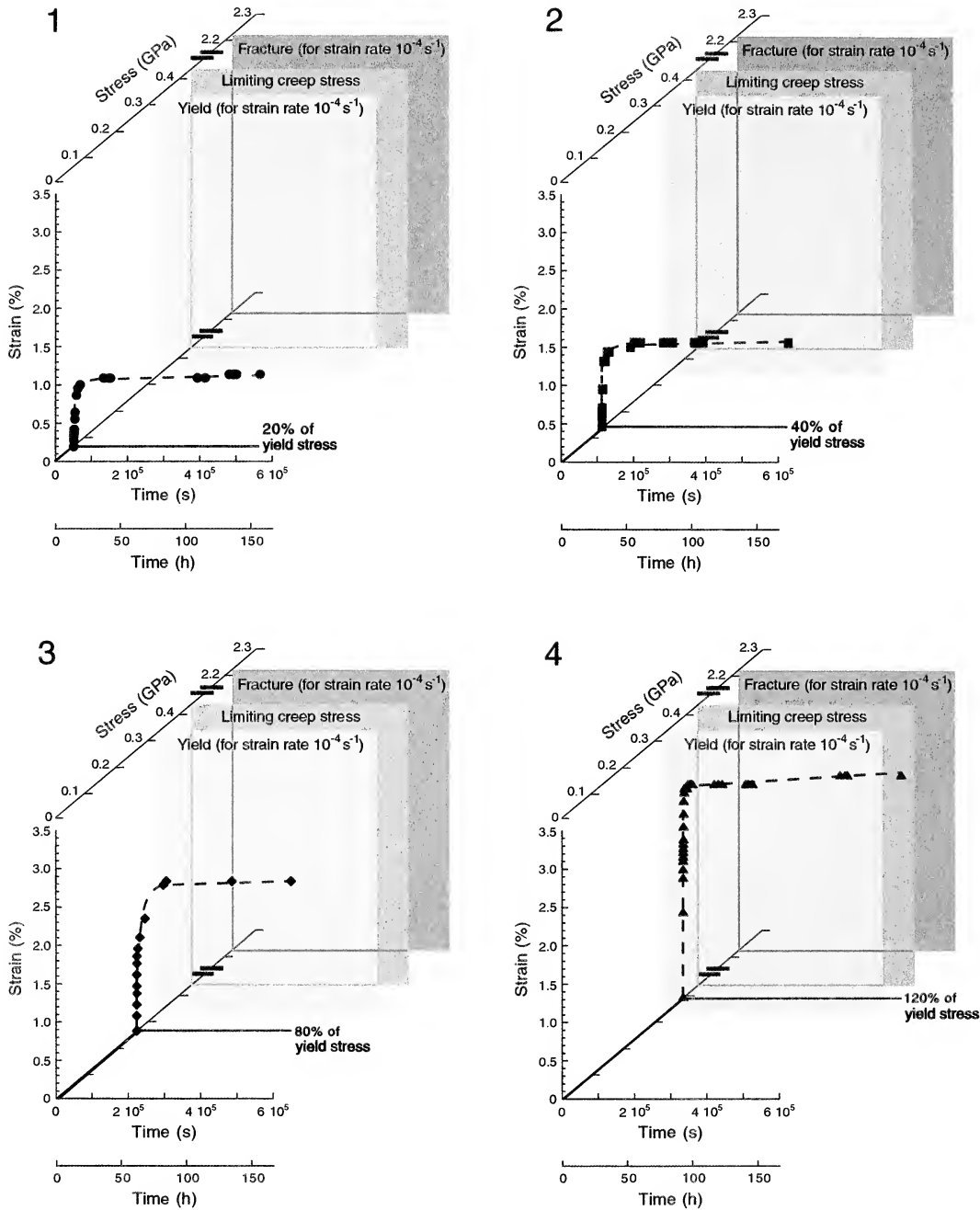
The tests that are routinely used to characterize the tensile properties of silk and other fibers are performed at a uniform strain (elongation) rate (Viney 2000b), of the order of 10^{-4} s^{-1} . In other words, the specimen is forced to extend by 0.01% of its original length every second until it breaks (which typically occurs within 30 minutes of starting the test). The changing force needed to achieve the constant strain rate is recorded, and the force–elongation data are commonly re-scaled and presented in

the form of a stress–strain plot. Here stress is the force applied parallel to the length of the fibre, divided by the original cross-sectional area of the fibre; strain is the resultant difference between the present and original lengths of the fibre, divided by the original length of the fibre. Such plots are conventionally used to define the yield stress or yield strength of the material, where the behavior deviates significantly from the initially linear relationship between stress and strain. If the test is interrupted and the load is removed before the yield stress is reached, the sample returns to its original length almost immediately, i.e. the sample behaves in a predominantly elastic manner. If the test is continued until the yield stress is exceeded, subsequent removal of the load does not result in immediate recovery of the original length; indeed, the original length may never be recovered. Stress-strain plots are also used conventionally to define the fracture stress or fracture strength of the fibre, in other words the stress at which the fibre breaks.

However, there are few instances where fibers would actually be subjected to a constant strain rate while in use. A more practical application might involve fibers being required to maintain a given tension, or carry a particular load, over an extended period of time. Under such circumstances, it becomes necessary to consider the time-dependence of the stress-strain behavior. Fibers subjected to a fixed load (and therefore fixed stress) for long times can respond with a gradual, continuous increase in strain until they break; even if the stress is signifi-

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Figures 1–4.—Creep behavior of *N. clavipes* dragline tested in air under ambient conditions. In each case, plot symbols and dashed lines show creep (strain vs time), and a solid line shows the corresponding stress history (stress vs time). Each experiment was performed over a period of at least 100 hours. Shaded planes mark the yield stress (measured at a strain rate of 10^{-4} s^{-1}), and also draw attention to the existence of a limiting creep stress as defined in the text. 1. Applied stress is 20% of yield stress. 2. Applied stress is 40% of yield stress. 3. Applied stress is 80% of yield stress. 4. Applied stress is 120% of yield stress.

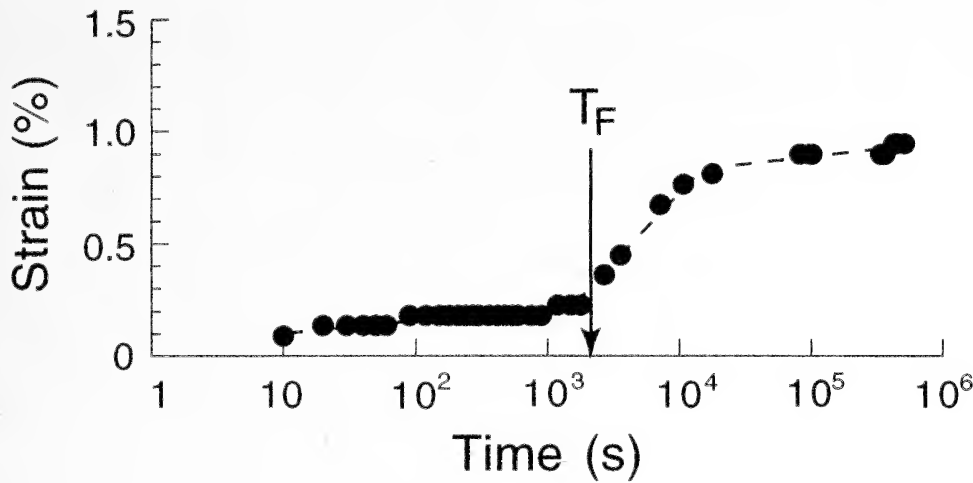


Figure 5.—Creep curve for sample loaded to 20% of yield stress (Fig. 1), re-scaled on a logarithmic time axis so that the initial stages of creep are emphasised. T_F is the approximate duration of conventional tensile tests performed on spider dragline at a constant strain rate of 10^{-4} s^{-1} ; such tests are typically completed (the fiber fails by breaking) in less time than it takes for creep to make its most significant contribution.

cantly less than the breaking stress or even the yield stress as defined above. This deformation to failure at constant stress is referred to as creep. We have previously shown (Bell et al. 2002) that the tension due to supercontraction (Work 1981) decreases rapidly in restrained dragline when it is wet, with the implication that wet silk will also undergo significant creep under constant load. The results presented below explicitly reveal an even stricter limitation on the possible applications of silk and its biomimetic analogues: creep can occur even at ambient humidity, and even if the applied stress is small.

Nephila clavipes (Linnaeus 1767) (Araneae, Tetragnathidae) spiders were provided by Angela Choate, University of Florida, Gainesville, FL; identification was confirmed by Dr Scott Stockwell at the US Army Research Development and Engineering Center (Mello et al. 1995). Major ampullate silk was reeled (Work & Emerson 1982; Thiel et al. 1994) from spiders at 1 cm s^{-1} , which corresponds approximately to the rate at which the silk is spun during web construction. Spiders were not anesthetized. Silk was stored on cardboard supports (Carmichael & Viney 1999) and kept in sealed containers in the dark until needed for testing. The silk retains its molecular organization, and therefore its physical properties, indefinitely when stored under these conditions. We used conventional constant strain rate tests, performed at 10^{-4} s^{-1} , to determine the average yield stress and fracture stress of the silk. To quantify the creep characteristics, we then set up a series of experiments in which a small load, a block of an appropriate number of staples, was carefully suspended from a length of single-fila-

ment fiber inside a vertical glass tube that provided a shield against draughts. The initial length (gauge length) of the fiber samples was approximately 20 cm; this is an order of magnitude longer than the gauge length which is used in constant strain rate tests (Viney 2000b), but is necessary here in order to provide readily measurable extensions during creep. The weight of the staples was chosen to apply a set percentage of the yield stress to the fiber. (Although we are interested in conditions that cause the fiber to break, it is conventional to quantify creep stress in relation to yield stress.) The staples were attached to the fibre with a small dab of cyanoacrylate superglue. At the start of each experiment the silk sample was straight but not under load, with the staples resting on a support that could be withdrawn smoothly and quickly through the lower end of the glass tube. A combination of millimeter-grid graph paper attached to the glass tube and a vernier cathetometer standing on the benchtop allowed sample extension to be monitored as a function of time. Ambient conditions were $19 \pm 2^\circ \text{C}$ and $60 \pm 5\%$ relative humidity. Creep experiments were performed three times at each value of applied stress, to take account of the intrinsic variability of dragline tensile properties (Pérez-Rigueiro et al. 2001); in each case data from the sample that survived for the median lifetime are displayed in Figs. 1–4.

Two notable observations emerge from this study. First, we can define a limiting creep stress: if samples are loaded smoothly and quickly to a constant stress lying above the limiting creep stress, they break within a few seconds of the stress being applied. The magnitude of the limiting creep stress

is equal to approximately one fifth of the fracture stress that we recorded in conventional constant strain rate tests. Secondly, creep is significant at stresses that are small compared to the conventional yield strength. This behavior becomes especially apparent over timescales that are not accessed in typical constant strain rate tests, as emphasised in Fig. 5.

We chose *N. clavipes* dragline for our study because this material has been used widely in several laboratories where the mechanical properties of spider silk are characterized; albeit at constant strain rate rather than our present condition of constant load. Whether our observations of its creep behavior are broadly representative of spider dragline in general remains to be explored, given that similar silks from different species can exhibit markedly different mechanical properties (Viney 2000a). The effects of temperature and humidity on creep behavior also require further study. Conditions recorded in the present work are representative of those within the daily range experienced by *N. clavipes*, at any time of year, in its native habitat in Gainesville, Florida (US National Climatic Data Center, www.ncdc.noaa.gov).

Our observations expose limitations of unmodified spider dragline silk (and any fully biomimetic analogues) for applications in which high unidirectional loads must be supported for long times without failure or continuously increasing deflection. The fact that native dragline is made up of molecularly interconnected crystalline and amorphous zones in series (Viney 2000b) is consistent with the propensity of the material to creep. A similar microstructural susceptibility to creep is exhibited by so-called "ultrastrong" polyethylene (USPE) fibers such as Spectra (Prevorsek 1995). This study highlights a need for caution when transferring lessons from Nature to technology. Silks that are designed for a natural in-service lifetime of minutes (e.g. major ampullate silk used as dragline) or days (e.g. major ampullate silk used as web frame silk) should not be expected to necessarily exhibit properties that will be retained over timescales relevant to high-tensile engineering materials.

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SHORT COMMUNICATION

HUNGRY SPIDERS AREN'T AFRAID OF THE BIG BAD WOLF SPIDER

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ABSTRACT. Foraging behavior in spiders can be influenced by a variety of factors. Here we investigate the effects of hunger and predation risk on feeding behavior in the wolf spider *Pardosa milvina* (Hentz 1877) (Araneae, Lycosidae). *Pardosa milvina* is preyed upon by the larger wolf spider, *Hogna helluo* (Walckenaer 1837), and responds with appropriate antipredator behavior to the silk and feces of this species. We predicted that hungry *Pardosa milvina* would be more likely to forage and consume prey under predation risk than satiated individuals. We found that hungry *Pardosa* under predation risk consumed as many prey as spiders not under predation risk. However, satiated *Pardosa* consumed significantly fewer prey when under predation risk. Our data suggest that the animal's energetic needs are weighed against the risks of foraging when predators may be present.

Keywords: Wolf spider, predation risk, hunger, foraging

The fitness of an animal, especially spiders, can be influenced by its foraging success (e.g. Uetz 1992). Often, foraging decisions that result in very high rewards are not the safest and animals weigh their current needs versus the level of risk involved (Lima & Dill 1990). That is, animals that are in need of energy will be more willing to take risks while foraging compared to well-fed or satiated animals (reviewed in Lima 1998a, b). Previous research has demonstrated that *Pardosa milvina* (Hentz 1877) is sensitive to predation risk (Persons & Rypstra 2001; Persons et al. 2001, 2002) and that individuals are not sensitive to changes in their energetic state as a result of decreased foraging success (Walker et al. 1999). However, we have not examined how changes in energetic state influence an individual's response to predation risk.

Pardosa milvina is a common cursorial spider in agricultural systems and early successional habitats throughout the eastern United States (Dondale & Redner 1990; Marshall & Rypstra 1999). *Pardosa milvina* is frequently preyed upon by the much larger wolf spider *Hogna helluo* (Walckenaer 1837) and exhibits behaviors that reduce its level of predation risk in the presence of silk and excreta from the much larger *H. helluo* (Persons & Rypstra 2001;

Persons et al. 2001, 2002). *Pardosa milvina* reduces its locomotor activity when on and avoids substrates that contain silk and excreta from *H. helluo* (Persons & Rypstra 2001; Persons et al. 2001, 2002). These behaviors result in increased survival of *P. milvina* in the presence of *H. helluo* even though they result in decreased feeding and reproductive success (Persons et al. 2001, 2002). Manipulating foraging success in *P. milvina* results in changes in body condition and presumably hunger in *P. milvina*, but does not affect locomotor activity (Walker et al. 1999). However we do not know if *P. milvina* will weigh its current energetic needs (e.g., a state of "hungry" versus a state of "satiated") when simultaneously faced with avoiding a predator and capturing prey. We conducted laboratory experiments to determine if predation risk and hunger simultaneously influence the number of prey captured by *P. milvina*.

For all experiments, subadult *P. milvina* were collected in May of 1998 from soybean fields at Miami University's Ecology Research center (Oxford, Butler County, Ohio, USA) and then raised in the lab to maturity. *Hogna helluo* used in this study were lab-reared offspring of individuals collected the previous year from the Ecology Research Center. Vouchers of both species are available from the Hefner Zoology Museum at Miami University. *Pardosa milvina* were maintained in 5.5 cm high × 5.5 cm diameter plastic containers and *H. helluo* were

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Table 1.—Mean number of fruit flies (S.E. in parenthesis) consumed by *P. milvina* in different treatments. Significant differences between treatments are denoted by different letters.

Hunger level	Predation risk	n	Number of flies consumed
Low	High	10	2.0 (0.17) A
High	High	10	3.4 (0.34) C
Low	None	8	4.7 (0.22) B
High	None	9	4.3 (0.37) BC

maintained in 8 cm high × 12 cm diameter containers (Walker et al. 1999; Persons et al. 2001, 2002). The bottom of all containers was filled with damp peat moss. Both species were maintained on a diet of domestic crickets (*Acheta domesticus* (Linnaeus 1758)).

To determine if *P. milvina* prey consumption was influenced by hunger and predation risk we counted the number of vestigial winged fruit flies (*Drosophila melanogaster* Meigen 1830), out of 5, consumed by individuals at different levels of hunger and predation risk in a 2 × 2 factorial design. To begin, we standardized hunger level by feeding animals to satiation. One group was then fed three times over the following week and the other was not fed at all. This manipulation results in changes in body condition (e.g. fasted animals are have lower body condition than animals in the high food treatment) and if we assume that this morphological indicator reflects internal state, then fasted animals should be hungrier than animals receiving food (see Walker et al. 1999). Predation risk was manipulated by moving spiders from their original containers to same sized containers (e.g., 5.5 cm × 5.5 cm) that either previously contained or never contained an adult female *H. helluo* for the previous 24 hours. This protocol, which places individual *P. milvina* in close proximity to the silk and excreta of *H. helluo*, is similar to what we have used in other studies to convey predation risk to *P. milvina* (Persons et al. 2001; 2002). We then added 5 fruit flies to each container and recorded the number captured and consumed over the next 1.5 h (see Persons et al. 2002). A total of 37 individual *P. milvina* were used in these experiments. The number of individuals used in each treatment is shown in Table 1. The total number of fruit flies consumed by an individual spider was compared across treatments using a two-factor analysis of variance and post-hoc comparisons were done using a Tukey-Kramer procedure.

The two-factor ANOVA showed significant effects of predation risk ($F_{(1,33)} = 36.1, P < 0.0001$) and the interaction between hunger level and predation risk ($F_{(1,33)} = 9.64, P = 0.0039$). However,

there was no significant effect of hunger level ($F_{(1,33)} = 2.825, P = 0.1022$). Post-hoc comparisons showed that satiated spiders under predation risk consumed fewer flies than those not under predation risk; however, there was no significant difference between the number of flies consumed by hungry spiders under predation risk and hungry spiders not under predation risk (Table 1).

Research has repeatedly shown that *P. milvina* assesses and responds to the risks associated with predation (Persons & Rypstra 2001; Persons et al. 2001; 2002). In this study, we show that *P. milvina* are not only sensitive to predation risk but also their own energetic state when making foraging decisions. Hungry spiders are more willing to forage and capture prey under predation risk than are satiated spiders. These data add further support to the hypothesis that an animal's behavior is sensitive not only to predation risk but also energetic needs (for reviews Lima & Dill 1990; Lima 1998a, b).

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SHORT COMMUNICATION

WATER SURFACE LOCOMOTION BY SPIDERS: DISTINCT GAITS IN DIVERSE FAMILIES

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ABSTRACT. Pisaurids such as *Dolomedes triton* (Walckenaer 1837) are well known as inhabitants of ponds and streams and are adept at locomotion on the water surface. In a broad survey of water surface locomotion in spiders, we have found that most taxa do not use specialized gaits under these circumstances. However, some tetragnathids, araneids, and salticids (three families that are outside of the superfamily Lycosoidea to which the pisaurids belong) resemble *D. triton* to the extent that they do use specialized gaits when on the water surface. Of these, the tetragnathids are particularly accomplished at water surface locomotion, achieving velocities that exceed those of *D. triton* when it rows, but not when it gallops.

Keywords: Aquatic locomotion, gaits, Pisauridae, Tetragnathidae, Philodromidae, Salticidae, Araneidae, Lycosidae, Gnaphosidae

Spiders in the family Pisauridae typically frequent the edges of bodies of water and many of them rely on the water surface for foraging, escape from predators, and the detection and pursuit of mates. For these spiders, the perception of being on the surface of water elicits either a rowing gait or a galloping gait (Shultz 1987; Barnes & Barth 1991), the former used exclusively on water and under conditions that do not require rapid locomotion, and the latter used when speed is required. The natural contexts in which pisaurids use these gaits (McAlister 1959; Shultz 1987; Gorb & Barth 1994; Suter & Gruenwald 2000a, b) and their biomechanical properties (Suter et al. 1997; Suter & Wildman 1999) suggest that the ancestors of the pisaurids succeeded in part because of the efficacy of these specialized gaits. A number of other spider families also have representatives that frequent the edges of ponds and streams (e.g., Tetragnathidae) and still others, while strongly terrestrial in habit, must contend with periodic flooding (e.g., gnaphosids).

In the context of a broad study of the occurrence of pisaurid-like aquatic locomotion in the Araneae, we have noticed (a) that several families outside of the Lycosoidea (which includes the Pisauridae) contain members that exhibit a specialized aquatic gait different from that used by pisaurids, and (b) that

in some taxa the walking gait characteristic of most terrestrial spiders on land can work very well on the water surface. In what follows, we describe the specialized gaits of *Tetragnatha* spp. Latreille 1804 (Araneae, Tetragnathidae), *Dolomedes triton* (Walckenaer 1837) (Araneae, Pisauridae), two jumping spiders, *Habronattus hallani* (Richman 1973) and *Phidippus* sp. C.L. Koch 1846 (Araneae, Salticidae), two orb-weavers, *Neoscona* sp. Simon 1864 and *Larinioides* sp. Caporiacco 1934 (Araneae, Araneidae), and *Tibellus* sp. Simon 1875 (Araneae, Philodromidae). We follow those descriptions with an analysis of the efficacy of the gaits in contrast to the walking gaits used on water by *Geolycosa rogersi* Wallace 1942 (Araneae, Lycosidae) and *Herypyllus ecclesiasticus* Hentz 1832 (Araneae, Gnaphosidae). Voucher specimens are deposited in the Mississippi Entomological Museum at Mississippi State University, Starkville, Mississippi.

We studied the locomotion of the spiders by releasing each into a glass or plastic arena with a floor area of approximately 0.16 m² covered to a depth of at least 2 cm with water (tap water whenever distilled water was unavailable; surface tension differences between distilled and tap water are negligible in this context). Video images of the movements of each spider, captured from directly above

Table 1.—Gaits used in locomotion across the water surface. When a specialized gait is not employed all of the time, the usual alternative in each case is a gait resembling walking and thus scored as 0 0 0 0 (see text for explanation of scoring). Video clips of the aquatic locomotion of *D. triton*, *Tetragnatha* spp., a salticid, and *G. rogersi*, can be viewed at the following website: <http://faculty.vassar.edu/suter/comparisons/>. *For *Tibellus*, we are skeptical that this constitutes a gait specialized for aquatic locomotion (see text).

Taxon	Specialized aquatic gait	Leg-pair score	Incidence of specialized gait
<i>D. triton</i> Pisauridae	Legs I and IV held motionless; legs III and II, in that order, provide rowing propulsion, members of each pair sweeping in unison	1 1 1 1	Always
<i>Tetragnatha</i> spp. Tetragnathidae	Legs I sweep out and to the side, alternating, and provide propulsion; legs II, III, and IV move in alternation	0 0 0 0	Always
<i>Tibellus</i> sp. Philodromidae	Legs I, III, and IV move in alternation; legs II sweep out and to the side, in unison, but appear not to provide more propulsive power than do the other legs	0 1 0 0	Always*
Pooled salticids Salticidae	Legs III, in unison, sweep out and to the side, providing rowing propulsion; legs I and II also sweep, but with little power; legs IV trail behind	1 1 1 1	Occasional
Pooled araneids Araneidae	Legs II and I, in that order, provide rowing propulsion, members of each pair sweeping in unison; legs III also sweep in unison, but with little power; legs IV trail behind	1 1 1 1	Rare
<i>G. rogersi</i> Lycosidae	(terrestrial walking)	0 0 0 0	Never
<i>H. ecclesiasticus</i> Gnaphosidae	(terrestrial walking)	0 0 0 0	Never

the arena, were digitized at 250 frames/sec by a high-speed motion analysis system (MotionScope S series, Redlake Imaging Corporation) and then recorded in VHS format at 30 frames/sec (JVC HR-S5400U). The movements of the spiders, slowed to about 1/8 the natural speed, could be qualitatively analyzed on a video monitor. We performed more detailed measurements (e.g., of absolute velocity) via frame-by-frame analysis in NIH Image, an image analysis shareware product available from the National Institutes of Health (<http://rsb.info.nih.gov/nih-image/>). Detailed descriptions of the measurement method have been published elsewhere (Suter et al. 1997; Suter & Wildman 1999).

In our qualitative analyses, we considered the following: for each pair of legs, did the members of the pair move in unison or alternately, or were the legs held motionless relative to the body of the spider? In our analyses of velocity, we used the linear measurement tools in NIH Image to determine the distance traveled over several strides during relatively straight-line locomotion, and divided that distance by the elapsed time as shown in ms on the recorded high-speed images.

The rowing gait of *D. triton*, with which we were already familiar from earlier studies (e.g., Suter et al. 1997; Suter & Wildman 1999), can be charac-

terized as involving pair-wise rowing motions by legs III and II, in that order, while legs I and IV are held approximately motionless in front of and behind the spider, respectively. In contrast, when *D. triton* walks on land, it employs an alternating tetrapod gait (Barnes & Barth 1991; Shultz 1987) in which the members of a leg pair move alternately and all eight legs are involved in propulsion. When *D. triton* gallops across the water surface, only legs IV remain relatively motionless while the three anterior pairs of legs stroke approximately in unison. Thus in both of *D. triton*'s aquatic gaits, legs I are non-alternating (they are either still or move in unison), legs II and III move in unison, and legs IV are non-alternating. We found it useful in visualizing these gaits and in comparing other gaits to them, to assign the value 1 to a pair of legs if the members of the pair moved in unison or were still, and the value 0 to a pair of legs that moved alternately. Using that set of rules, both rowing and galloping by *D. triton* are scored as 1 1 1 1, whereas walking on land by the same animal is scored as 0 0 0 0.

Table 1 provides not only brief descriptions of the aquatic gaits employed by the species in this study but also leg-pair scores for these gaits. Note that the scores shown in the table ignore variability

within and between individuals because the purpose of the scores in this paper is to provide a shorthand characterization of specialized aquatic gaits rather than to evaluate the frequency with which they are used. A detailed analysis of gait variability will appear elsewhere (Stratton et al. in preparation). We have included in the table a column to provide a qualitative estimate of the incidence of each specialized gait. Video clips of the aquatic locomotion of representative taxa used in this study can be viewed at the following website: <http://faculty.vassar.edu/suter/comparisons/>.

We considered a gait to be specialized for aquatic locomotion if (a) it differed qualitatively from the gait used on land and (b) we could detect in the motions of the spider evidence that the novel leg motion produced thrust. On land, for example, *Tetragnatha* spp. move rather awkwardly, propelling forward in the alternating tetrapod gait that characterizes the locomotion of most spiders on solid substrates (Barnes & Barth, 1991; Shultz, 1987). On the water surface, the spider uses its legs in the same sequence (the members of each contralateral pair of legs alternating), but the locomotion is dominated by the alternating backward sweeps of the two anterior legs. Their motion is in the plane of the water surface (on land, their motion is in a plane nearly perpendicular to the substrate) and causes a pronounced, rhythmic "wag" in the animal's elongate body as the spider surges forward with the stroke of each leg. Thus the gait is qualitatively different from what is used on land and the sweep of each anterior leg causes a noticeable change in the motion of the spider (in this case, both a wag and a surge forward).

Criteria (a) and (b) were met by *Dolomedes triton*, *Tetragnatha* spp., by the salticids and by both species of araneids used in this study (note that many of the salticids and araneids we tested in the broad survey did not adopt qualitatively different gaits than those used on land). Among these, *Tetragnatha* spp. stands out because their aquatic gait involves legs in alternation, whereas the aquatic gaits of the others all involve propulsion by contralateral legs stroking in synchrony (Table 1).

In contrast, three of the species in this study, *Tibellus* sp., *G. rogersi* and *H. ecclesiasticus*, have only one gait on the water surface, and it is the same walking gait that these spiders use on land. Thus, criterion (a) was not met by these spiders. In this respect, *Tibellus* is particularly interesting because its aquatic gait resembles rowing with legs II. On the water surface, this spider walks with six legs (I, III, IV) in the alternating hexapod gait that characterizes land locomotion by insects. Legs II are longer and are held out to the sides, appearing to stroke backwards in unison. But their strokes do not result in surges in the forward motion of the spider, nor is there any other evidence that the movements

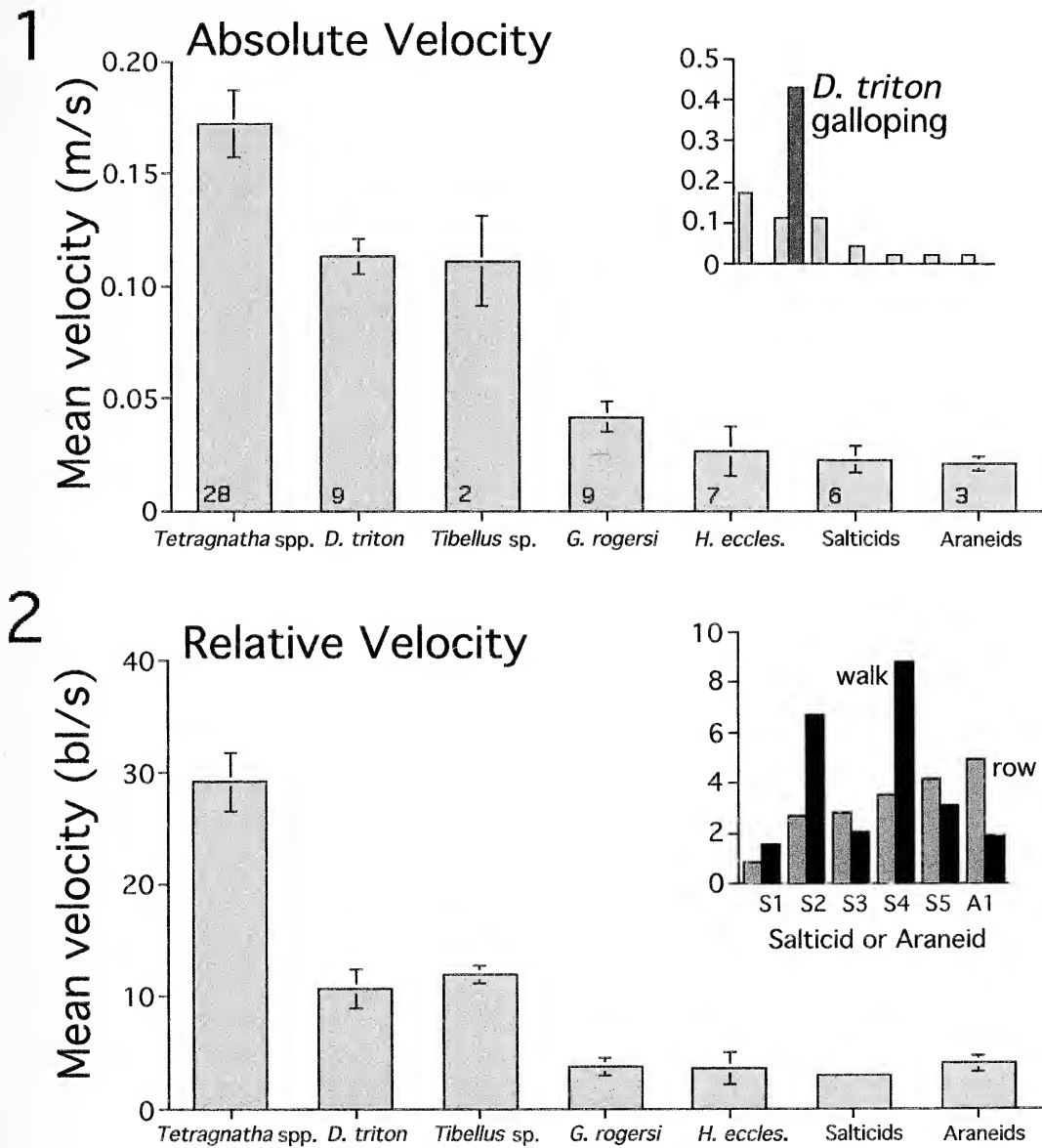
of these legs affect aquatic locomotion (c.f., criterion b). We studied videotapes of *Tibellus*'s locomotion on land and observed precisely the same pattern of leg motion (c.f., criterion a). We have tentatively concluded that, for this spider, legs II are used as antennae, monitoring the environment as it passes by to either side. Certainly we see no evidence that these legs function in propulsion on the water surface.

Absolute and relative velocities give some indication of the efficacy of locomotion, that is, how well it works. For the spiders in this study mean velocities ranged between 0.019 ± 0.010 m/s (mean \pm S.E.) and 0.172 ± 0.015 m/s (Fig. 1), and relative velocities ranged between 2.74 ± 1.26 body lengths per second and 29.13 ± 2.58 bl/s (Fig. 2). A parametric ANOVA on the absolute velocity data revealed significant ($P = 0.0001$) between-taxa variation. Post-hoc tests (Fisher's PLSD) showed that *Tetragnatha* spp. was significantly faster ($P < 0.05$) than each of the other taxa except *Tibellus* sp., and that *D. triton* was significantly faster ($P < 0.05$) than the salticids, the araneids, *G. rogersi* and *H. ecclesiasticus*. There were no significant absolute velocity differences among the five taxa excluding *Dolomedes* and *Tetragnatha*.

An ANOVA on the relative velocity data revealed significant ($P = 0.0001$) between-taxa variation. Post-hoc tests showed that *Tetragnatha* spp. was significantly faster ($P < 0.05$) than each of the other taxa, and that there were no other significant relative velocity differences.

Our assumption at the start of our investigation was that spiders such as *Tibellus* sp., *G. rogersi* and *H. ecclesiasticus*, which have the same walking gait on land and on the water, would underachieve when their aquatic locomotion was compared to that of spiders with specialized gaits. Why, otherwise, would specialized gaits have evolved? That rationale for the presence of specialized gaits is supported by our data on *Tetragnatha* spp. and *D. triton*, both of which perform significantly better in terms of absolute velocity than do the two non-specialists on which we have adequate data (*Tibellus* sp., with $n = 2$, deserves to be ignored). Additional support comes from the *Tetragnatha* spp. data on relative velocity. Given the fact that *D. triton* can also call upon a second aquatic gait, galloping (Suter & Wildman 1999; Fig. 1 inset) when high speed is required, it is reasonable to claim that the data from both of these "specialists" supports the adaptationist rationale for specialized aquatic gaits.

In contrast, the specialized aquatic gaits used rarely among araneids and occasionally among salticids (Table 1) appear to confer no obvious benefit: the absolute and relative velocities achieved by spiders using these rowing gaits are unremarkable when compared to the walking gaits used by *G. rogersi* and *H. ecclesiasticus*. To look more closely



Figures 1–2.—Velocities attained on water by spiders in seven diverse taxa. 1. Absolute velocities: bars represent means \pm S.E., with n shown at the base of each bar. The bar for *D. triton* represents the rowing gait only; the galloping gait for that species is shown for comparison as the darker bar in the inset. 2. Relative velocities expressed in body lengths per second. For a few individual spiders in the salticid and araneid samples, we also had data on walking (as opposed to a specialized aquatic gait) (inset); here the dark bars represent walking and the lighter bars represent rowing.

at the efficacy of these specialized gaits, we compared the relative velocities achieved by rowing to those achieved by walking in the five salticids and the one araneid in which the individual spiders used both gaits during our test runs (Fig. 2 inset). Even in these within-individual comparisons, the results are equivocal: three of the salticids walked on water

faster than they rowed, and two salticids and the one araneid rowed faster than they walked. Our data indicate that specialized aquatic gaits occur in at least three families (commonly in Tetragnathidae, but rarely in Salticidae and Araneidae) that are outside of the superfamily Lycosoidea. But only in tetragnathids (along with the pisaurids

which are part of the Lycosoidea) is the propulsion provided by the gait adequate to suggest that its use evolved because of its effectiveness. What remains is a conundrum: we have demonstrated the presence of behaviors in salticids and araneids that appear not to be advantageous to their performers. The rarity of these behaviors is certainly understandable in that context, but their persistence is not. Further investigations may reveal that physiological cost or some other as yet unmeasured parameter explains the presence of these not very effective aquatic gaits.

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SHORT COMMUNICATION

BURROW USE IN A NORTHERN CALIFORNIA POPULATION OF THE WOLF SPIDER *SCHIZOCOSA MCCOOKI* (ARANEAE, LYCOSIDAE)

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ABSTRACT. Observations on the wolf spider *Schizocosa mccooki* in northern California grasslands reveal previously unreported burrowing behavior, known to occur in only one other member of the genus. Adult and penultimate female *S. mccooki* may occupy burrows that vary widely in depth and the occurrence of silk linings. Mark-resight techniques revealed burrow fidelity spanning several weeks for individual spiders. Behaviors such as courtship and prey consumption can occur at, but are not restricted to, the entrances to these burrows. Burrows appear to offer daytime shelter for *S. mccooki*, though it remains unclear whether protection from predators or amelioration of abiotic conditions is the primary basis for burrow use.

Keywords: Burrow use, northern California, lycosids

Burrows may offer spiders protection from predators, amelioration of climatic stresses, and a concealed location from which to ambush prey. Burrowing has been reported in many genera of wolf spiders, and it appears to have evolved several times independently in the family Lycosidae. In North America, all the *Geolycosa* (Wallace 1942) and certain members of the *Arctosa* (Kaston 1948), *Alopecosa* (Emerton 1919), *Gladicosa* (Montgomery 1904; Brady 1986), *Hogna* (Wallace 1942; Shook 1978), *Rabidosa* (Kaston 1948) and *Schizocosa* (Dondale & Redner 1990) engage in some form of burrowing behavior. While some authors have presented burrowing as a conserved character at the generic level (Zyuzin 1990; Zehethofer & Sturnbauer 1998), it should be applied with caution as a trait for phylogenetic analysis; our understanding of the prevalence and form of this behavior across the subfamilies, genera, and species of Lycosidae is quite limited, and in some published reports is highly contradictory (e.g. Zyuzin 1990; Zehethofer & Sturnbauer 1998). Observations on the wolf spider *Schizocosa mccooki* (Montgomery 1904) highlight the current scientific ambiguity over this behavior.

Kaston (1972) states that members of the genus *Schizocosa* “do not dig holes in the ground, but are found running about over the surface.” Dondale & Redner (1990), however, report burrow construction and use by large juveniles and adult females in Canadian populations of *Schizocosa avida* (Walckenaer 1837). To date, this is the only report of burrow

use in the genus. I report here on observations of burrow use and measures of burrow fidelity in a northern California population of *S. mccooki*.

Schizocosa mccooki is a widespread, medium-sized wolf spider, with female length 9.6–22.7 mm (Dondale & Redner 1990). It occurs from the Yukon Territory and British Columbia south to Mexico and east to Texas, Michigan, and Ontario (Dondale & Redner 1978, 1990). Habitat association in *S. mccooki* varies with geographic locale; the species has been collected in dry grassland in Saskatchewan (Buckle 1972), in sagebrush meadows in Idaho (Allred 1975), among grasses and sedges on sand dunes on the shores of Lake Erie (Dondale & Redner 1978), on open ground and desert shrubs in pinyon pine-juniper woodland in New Mexico (Stratton and Lowrie 1984) and in grass and mixed-grass/shrub habitats in the shortgrass steppe in Colorado (Weeks & Holtzer 2000). It has never been reported to use burrows.

Schizocosa mccooki is abundant and widespread at the Angelo Coast Range Reserve in Mendocino County, California (39°43′45″N, 123°38′40″W; elevation ca. 400 m). The Reserve covers over 3000 hectares of protected old-growth Douglas fir and redwood forest, interspersed with mixed oak woodland and grassy meadows along a 5 km reach of the South Fork Eel River. *Schizocosa mccooki* occurs primarily in the meadows and along the meadow-forest boundary, but it has also been observed in forest and riparian habitats. Mature males are found from early June through August and mature

females are common from early June to mid-September and have been found as late as November.

During the summers of 1999–2002, I observed a total of 41 individuals partially concealed in burrows (Fig. 1), defined here as excavated retreats in the soil with diameter 7–18 mm. Although wolf spiders commonly retreat under cover and into crevices and holes when pursued for collection, these were all unmolested individuals. All *S. mccooki* observed in burrows were penultimate and adult females, many carrying egg sacs. One individual was observed consuming a katydid (Orthoptera, Tettigoniidae) at the entrance to a burrow and another a crane fly (Diptera, Tipulidae). Courtship took place at another burrow; a male faced a female partially concealed in the burrow from a distance of approximately two centimeters and performed palpal movements similar to those described in Stratton & Lowrie (1984). All burrows were in the meadow or along the meadow-forest margin, and many were lined with silk (Fig. 2). The 41 females I observed in burrows composed a small percentage (< 10%) of the total number of individuals observed in surveys ($n > 430$). Most female and all male *S. mccooki* observed in the field were wandering on the ground.

After initial observations of burrow-inhabiting individuals in the summer of 1999, I subsequently observed marked individuals to determine whether burrows were occupied briefly, in the course of a night's foraging, or consistently, as a central-place refuge. During the summer of 2000 and 2001, I recorded all instances of burrow use observed in *S. mccooki* and measured the duration of burrow occupancy. Whenever I found a spider in or immediately adjacent to a burrow, I marked the burrow with a flag and the female's anterior legs with fluorescent powder. The powder was sprayed from a distance of several centimeters through a modified syringe to minimize disturbance to the spider. I re-examined burrow entrances each of the next two nights, and then on nights five, six, ten, 11, 20 and 21. I conducted the surveys at night because I found that spiders occupied burrow entrances more commonly at night than during the day.

I marked a total of 16 burrows and occupant females on eight nights in June and July 2000 and 2001. The original spiders occupied the entrances to 13 of these burrows during the next two nights, 11 of the burrows on nights five and six, nine on nights ten and eleven, and three on nights 20 and 21. It is unknown whether individuals absent from burrow entrances were concealed inside, wandering outside, or dead.

To help resolve this question and to examine burrow architecture, I excavated 12 burrows with a hand shovel the day after observing an individual at a burrow entrance in August 2002. Burrows ranged from 6–21 cm in depth, and none were

branched. I excavated six of these burrows in the early afternoon and six in the late evening. I located spiders concealed inside five of the six burrows excavated in the afternoon, suggesting that burrows provide daytime shelter to *S. mccooki*. The evening excavations revealed spiders at the entrances to two burrows, concealed inside one burrow, and absent altogether from three burrows. This suggests that *S. mccooki* may wander and return rather than occupy burrows continuously, however no dye-marked individuals in the previous two summers were observed away from burrows.

Although many female *S. mccooki* were seen in and adjacent to burrows, no excavatory activity was ever observed. It thus remains uncertain whether *S. mccooki* is a primary excavator or a facultative user of burrows excavated by similarly sized organisms such as wasps. No other burrowing wolf spiders are known at the study area. The obligate burrowing Antrodiaetid, *Atypoides riversi* (O.P.-Cambridge 1883), is common in the study area, but its burrows have distinct turrets and several branches and are found on steeper forested slopes, so there is no fine-scale range overlap with burrows of *S. mccooki*.

While the prevalence and purpose of burrow use in *S. mccooki* are unclear, its existence in this population is certain. Burrow use has been documented in populations of the very closely related *S. avida* (Dondale & Redner 1990), but in no other congeneric species. It has further been documented in many other genera of wolf spiders in a variety of forms. Depending on the species, burrows can range from deep, silk-lined tubes with protruding turrets to simple, shallow depressions. They may be used by both sexes throughout life or by females of only certain age classes. Wolf spiders may live in and hunt from burrows, they may live in burrows but wander outside in search of prey, or they may use burrows just when molting or constructing an egg sac. Clearly, a great deal of uncertainty remains over this highly variable behavior. Further study is needed to clarify the prevalence and purpose of burrow use in wolf spiders and any implications for lineage evolution.

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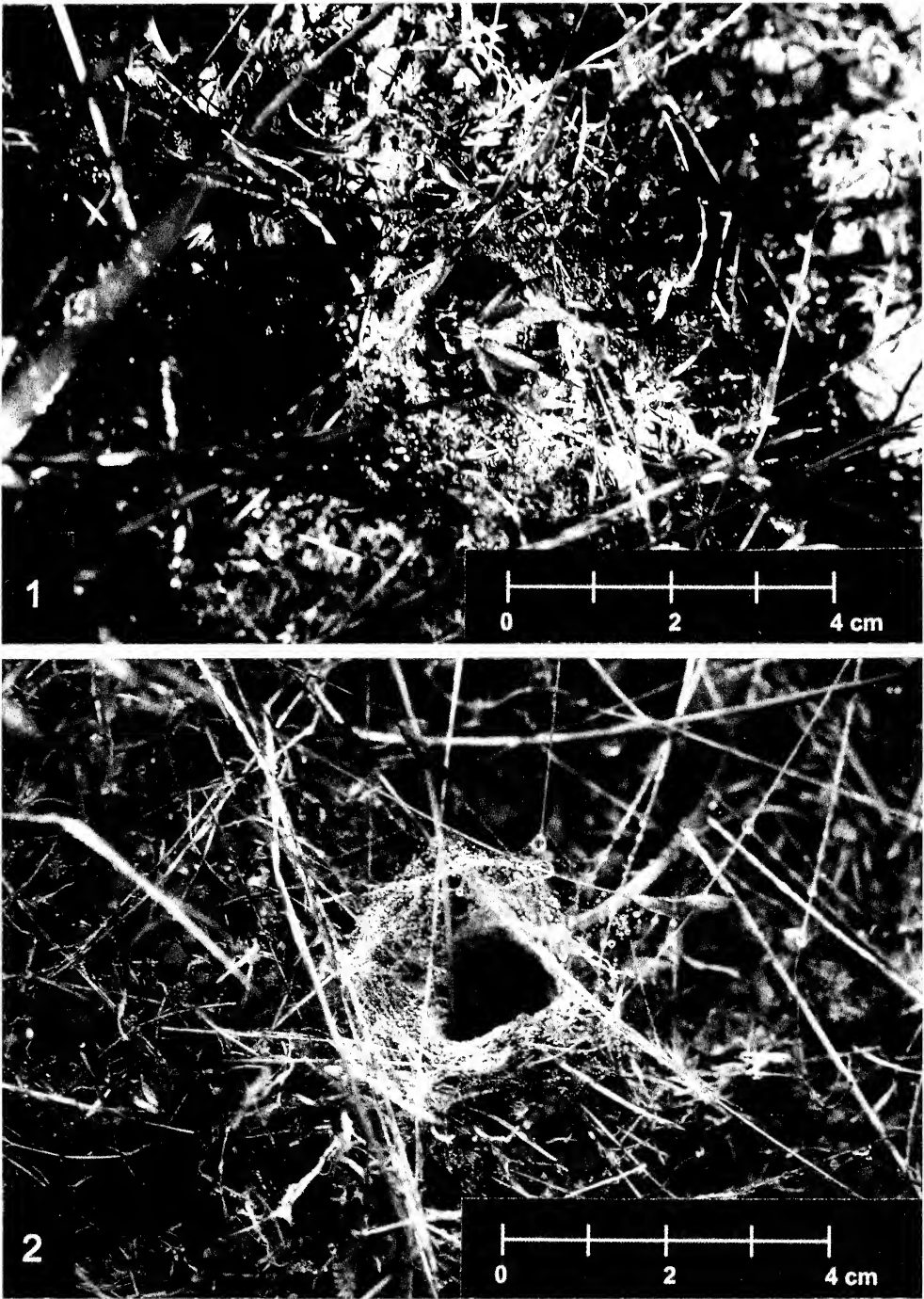


Figure 1.—An adult female with egg sac sits partially concealed in the entrance to her burrow.
Figure 2.—The silk linings of this burrow are made clearly visible by early morning dew.

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SHORT COMMUNICATION

TREES USED FOR TUBE SUPPORT BY *SPHODROS RUFIPES* (LATREILLE 1829)(ARANEAE, ATYPIDAE) IN NORTHWESTERN LOUISIANA

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ABSTRACT. Little information is available concerning the tree species preferred by the American red-legged purseweb spider, *Sphodros rufipes* (Latreille 1829), for supporting their webs. During a study of the spiders of northwestern Louisiana, 26 pursewebs of *S. rufipes* were found. All were on deciduous trees, with 58% found on sweetgum or oak. None of the webs were on conifers or herbaceous plants even though conifers made up 7–92% of the trees in the sampled areas. All pursewebs were within 20 m of a stream and were on trees with a trunk less than 70 cm dbh.

Keywords: Purseweb, habitat, hardwoods, habitat preference, web placement

Sphodros Walckenaer 1835 contains seven species which are collectively known as the American purseweb spiders. The genus is distributed in eastern North America, from southern Ontario, through the eastern United States to Texas and northeastern Mexico. The following six species have restricted geographic distributions: *S. abboti* Walckenaer 1835 (restricted to southern Georgia and northern Florida in hammocks and mesic situations), *S. atlanticus* Gertsch & Platnick 1980 (found in Georgia, Illinois, North Carolina, and Virginia, forests), *S. coylei* Gertsch & Platnick 1980 (known only from South Carolina, mixed forest), *S. fitchi* Gertsch & Platnick 1980 (from Nebraska, Kansas, Oklahoma, and Arkansas, deciduous forest, grassland), *S. niger* (Hentz 1842) (northeastern U.S. and southern Ontario, habitat unknown [see below]), and *S. paisano* Gertsch & Platnick 1980 (southeastern Texas and northeastern Mexico, habitat unknown). Within the genus *Sphodros*, the first species described was *Sphodros rufipes* (Latreille 1829), which also has the largest geographic distribution (southeastern U.S. from Rhode Island into Louisiana and eastern Texas) and is the only species known from Louisiana. All of the specimens examined from northwestern Louisiana are *S. rufipes*.

Sphodros rufipes, the American red-legged purseweb spider, is usually found in mixed pine-deciduous forest and is uncommon throughout its geographic distribution in North America. While some information is available about the general biology of *S. rufipes*, such as its dramatic method of prey capture (Comstock 1965), few details are known about its habitat requirements and reproduc-

tion anywhere in its range. The pursewebs of *S. rufipes* are vertical tubes with the upper end of the tube attached to a tree, a rock, or even a concrete wall, and the lower end embedded several cm into the soil (McCook 1888).

The only information about the pursewebs of *S. rufipes* in Louisiana is from Gertsch & Platnick (1980), who collected a total of four specimens from four separate localities in Louisiana. The web of one of those specimens was on a cliff, one was on an oak tree (*Quercus*), and one was on a beech tree (*Fagus grandifolia*); no habitat was given for the fourth specimen. No other tree species was given for supporting the aerial web of *S. rufipes* out of 94 specimens (from throughout the geographic range) listed by Gertsch & Platnick (1980).

During a continuing survey of the spiders of northwestern Louisiana, several specimens of *S. rufipes* were found. The most effective search strategy for this rare species was to look for their very distinctive webs. It was quickly discovered that certain mixed pine-deciduous forest habitats produced many more pursewebs of *S. rufipes* than did others. There are few references concerning the tree species preferred by any species of *Sphodros* for the support of the pursewebs, and no references have reported the spider's preferences for hardwoods versus pines as web support structures.

Poteat (1889) reported a large population of *S. niger* in a pine forest in Wake Forest, North Carolina, and described the attachment of a purseweb (2 cm wide at the ground, 15 cm tall) to a small pine. Of 30 pursewebs Poteat (1889) found in (or near) a 900 sq. yd. (754.8 sq. m) area during three years,

28 were attached to pines (3–35 cm diameter; species not given), one was on a very small persimmon (*Diospyros virginiana*) and the other was on a wild rose (*Rosa* sp.); all were vertical. The spiders studied by Poteat (1889) were well within the geographic range of the more common *S. rufipes*. The locality is also within the geographic range of the less common *S. atlanticus*, but is just southeast of the known geographic range of *S. niger*. Therefore, it is likely that Poteat's population was *S. rufipes*. The current status of Poteat's specimens is not known and they were not seen by Gertsch & Platnick (1980).

Bishop (1950) found only vertical pursewebs in Florida and agreed that the Poteat specimens were *S. milberti* Walckenaer (1837 [= *S. rufipes*]); however, Bishop did not mention the species of plants used to support the webs of spiders in his study.

Gertsch & Platnick (1980) doubted that all American *Sphodros* construct vertical tubes and suggested that *S. niger* does not. However, pursewebs that are horizontal to the ground surface, without a vertical aerial component, have not yet been documented in any species of *Sphodros*. Sarno (1973) described the tops of the pursewebs of *Atypus snetsingeri* Sarno 1973 in Pennsylvania as attached to lower stems and roots of a hedgerow, small magnolias, rhododendron, and a concrete foundation. Her references to the "tops" of the pursewebs attached to the plants and their lengths of 150–175 mm "above the surface of the soil, and the burrows from 100–150 mm below" clearly indicate a vertical aerial tube. Her mention of horizontal pursewebs is only for captive specimens in containers (Sarno 1973). Gertsch & Platnick (1980) incorrectly comment that although Sarno (1973) reported that her captive specimens of *Atypus snetsingeri* Sarno 1973 "resemble their European counterparts in building horizontal tubes along the surface of the ground, her description of the tubes in nature does not specify their orientation." Sarno never mentioned any comparison with European counterparts.

The excellent work by McCook (1888) on the pursewebs of *S. abboti* reports only vertical pursewebs and that *S. abboti* had no preference for any special tree. Gertsch (1936) reported only vertical pursewebs of *S. abboti* on sweet gums, oaks, and magnolias in Florida. Chamberlin and Ivie (1944) reported pursewebs on trees and that *S. abboti* tends to occur in colonies in Georgia. Muma & Muma (1945) studied 33 pursewebs of *S. bicolor* (= *S. rufipes*) in Maryland; there was no mention of any horizontal tube nor of the identity of the trees used.

The paucity of details on the species of trees used for web support and the confusions noted above concerning the webs of American purseweb spiders indicated the need for additional information. The objectives of this project were to, 1) document the species and size of trees used as web supports for

Sphodros rufipes in northwestern Louisiana, and 2) to determine if pine trees or hardwood trees are equally utilized by *S. rufipes* in northwestern Louisiana.

Specimens and pursewebs of *S. rufipes* were studied in several locations in Caddo, Winn and Grant Parishes, Louisiana, during 1996–2000 (see Specimens Examined). Purseweb spiders in northwestern Louisiana are found in contiguous mixed pine-deciduous secondary forest in bottomland areas, often in the vicinity of temporary or permanent water. In this region they are uncommon; however, due to the more durable web structure, the webs were found during all seasons of the year. When pursewebs were found, each was checked for a resident spider. The tree species and DBH (diameter at 4.5 feet from the base of the trunk, cm) were determined. The distance between the tree and the nearest stream was measured in some cases. All specimens examined are in the spider collection of the Museum of Life Sciences of Louisiana State University in Shreveport (LSUS).

To determine if individuals of *Sphodros rufipes* were selecting hardwoods over pines, it was necessary to determine the relative availability of pines and hardwoods in the forests that contained *S. rufipes*. To determine if pines and hardwoods were equally available for purseweb construction in the immediate vicinity of active pursewebs, I recorded the numbers of pines and hardwoods (15 cm DBH or larger) in four transects from each of five different localities (a total of 20 transects) that were at locations where 11 spiders were collected. At each locality the census transects consisted of four 2 m wide lanes, 50 m long, radiating at 0, 90, 180 and 270 degrees from the center (a total of 400 sq. m censused per locality).

A total of 26 pursewebs were found on 24 trees of 11 species (Table 1). The mean DBH of the 21 trees that were measured and that supported pursewebs was 20.9 cm (range = 3–65; median = 13).

Fifty-four percent (13 of 24) of the trees containing pursewebs and 58% (15 of 26) of all pursewebs were on *Liquidambar* or *Quercus* (Table 1). However, 50% (7 of 14) of all spiders were found on the other nine species of trees and only 21% (3 of 14) were found on *Quercus* (Table 1). Fifteen pursewebs (68% of the 22 tubes) did not contain spiders. The only trees with two pursewebs were one *Liquidambar* and one *Quercus*. All spiders were in pursewebs on trees less than 36 cm DBH. The mean tree DBH for occupied pursewebs was 17.3 cm (range = 3–35; median = 13; $n = 10$). The trees bearing empty pursewebs were as large as 65 cm and at one time were used by a resident spider. Most of the trees that supported pursewebs were less than 0.5 m dbh, but all were well rooted saplings or larger (Fig. 1). None of the pursewebs was on grass or other herbaceous plants, even

Table 1.—Characteristics of support trees for 26 pursewebs of *Sphodros rufipes* from northwestern Louisiana.^{1,2} Two pursewebs were on the same tree.³ 25 cm is the maximum size of 3 different trees, other measurements were not recorded; this was counted as one tree in calculations.

Tree	DBH (cm)	Date	Notes
<i>Liquidambar styraciflua</i>	13	10 Nov. 1996	Spider in tube 10–15 cm long
<i>Liquidambar styraciflua</i>	30	10 Nov. 1996	Spider in flat tube 24 mm wide
<i>Liquidambar styraciflua</i>	11 ¹	21 Nov. 1996	
<i>Liquidambar styraciflua</i>	11 ¹	21 Nov. 1996	
<i>Liquidambar styraciflua</i>	10	21 Nov. 1996	Tube forked
<i>Liquidambar styraciflua</i>	16	21 Nov. 1996	
<i>Liquidambar styraciflua</i>	12.5	20 May 1999	Spider in tube
<i>Quercus falcata</i>	32 ²	21 Nov. 1996	
<i>Quercus falcata</i>	32 ²	21 Nov. 1996	
<i>Quercus falcata</i>	56	21 Nov. 1996	
<i>Quercus velutina</i>	65	21 Nov. 1996	
<i>Quercus alba</i>	—	13 July 1999	Spider in tube
<i>Quercus nigra</i>	23	21 Nov. 1996	
<i>Quercus</i> sp.	35	16 May 2000	Spider in tube
<i>Quercus/Elmus</i> (3 trees)	25 ³	3 Nov. 1996	4 spiders, 1 tube/tree, 1 tube w/2 spiders
<i>Acer saccharum</i>	24	21 Nov. 1996	Spider in tube
<i>Acer saccharum</i>	5	21 Nov. 1996	Spider in tube
<i>Carpinus carolinianus</i>	3	21 Nov. 1996	Spider in tube
<i>Carpinus carolinianus</i>	6	21 Nov. 1996	
<i>Cornus florida</i>	5	21 Nov. 1996	
<i>Ilex opaca</i>	—	10 May 2000	Spider found in tube
<i>Ostrya virginiana</i>	12	21 Nov. 1996	Spider found in tube
Small tree		21 June 2000	
Unknown	13	29 Nov. 2000	Spider found in tube

though such herbaceous plants were present in the immediate vicinity of active pursewebs.

Twenty 50 m transects contained 73 hardwoods and 34 pines. The mean frequency of pines per transect was 45.2% (range = 0–92.3%; *n* = 20). Within the five localities studied, pines represented 7.1–

92.3% of the sampled trees. Therefore, pines (*Pinus taeda* L., Loblolly; *P. echinata* Miller, Shortleaf; *P. palustris* Miller, Longleaf; and *P. elliotii* Engelman, Slash) were readily available at all localities, but were not used by *Sphodros rufipes* for web support.

If *Sphodros* was using hardwoods and pines with equal frequency, based on the relative abundance of each tree type, then the frequencies of pursewebs on pines should be the same as the frequency of pines in the forest surrounding the web.

In northwestern Louisiana the pursewebs of *S. rufipes* are on hardwoods of moderate size (less than a meter, DBH; Fig. 1). None was found on pines or herbaceous plants. The loose, flaky nature of pine bark is probably detrimental to the long-term survival of the pursewebs. All pursewebs were found in the vicinity of a stream (1–15 m from tree). In many of the examples reported here the pursewebs were found on the vertical back wall of the trunk between buttressed roots and the web below ground always curved under the center of the tree trunk.

Specimens of Spiders Examined (*n* = 15).—All localities are in Caddo Parish, Louisiana unless noted otherwise and all specimens are in the spider collection of the Museum of Life Sciences of Lou-

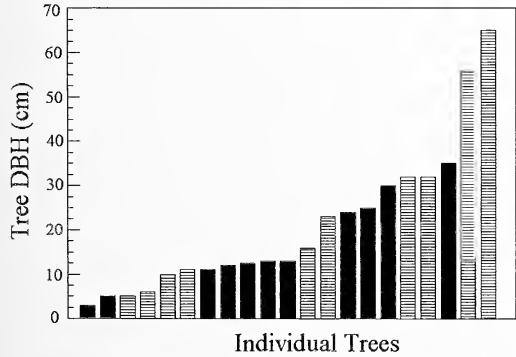


Figure 1.—Size (DBH in cm) distribution of trunks, from the smallest to the largest, that supported pursewebs of *S. rufipes*. Each bar represents an individual tree. The hatched bars represent unoccupied webs; the solid bars represent pursewebs that contained a spider.

isiana State University in Shreveport. 2.5 mi. W, 1.0 mi. S Blanchard, 3 Nov. 1996 (LMH 11708, ♀, total length [TL] = 17 mm; 11709, ♀, TL = 11; 11710, ♀, TL = 8; 11711, ♀), 21 Nov. 1996 (LMH 11744, ♀, TL = 13; 11745, ♀, TL = 12; 11746, ♀, TL = 12; 11747, ♀, TL = 10); 0.6 mi. W, 3.0 mi. N Keithville, 10 Nov. 1996 (LMH 11720, ♀, TL = 19, 11721, ♀, TL = 12); Winn Parish, 4.0 mi. E, 2.0 mi. S Goldonna, 10 May 2000 (LMH 12228, ♂, immature), 16 May 2000 (LMH 12244, ♀, TL = 11), 29 Nov. 2000 (LMH 12365, ♀, TL = 23); 5.0 mi. S, 2.3 mi. W Brewton Mill, 20 May 1999 (LMH 11957, ♀, TL = 19); Grant Parish, 3.8 mi. W, 3.2 mi. S Packton, 13 July 1999 (LMH 12090, ♀, TL = 12).

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SHORT COMMUNICATION

MALE EGG GUARDING BEHAVIOR IN THE NEOTROPICAL HARVESTMAN *AMPHERES LEUCOPHEUS* (MELLO-LEITÃO 1922) (OPILIONES, GONYLEPTIDAE)

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ABSTRACT. Males of the Neotropical harvestman *Ampheres leucopheus* (Mello-Leitão 1922) were observed guarding egg-batches attached to the undersurface of leaves. As recorded for other paternal harvestmen, males of *A. leucopheus* guard egg-batches containing eggs in different developmental stages as well as newly hatched nymphs. This is the second case of paternal care recorded among gonyleptids and the fifth in the order Opiliones.

Keywords: Harvestmen, Caelopyginae, parental care, postzygotic investment

Egg guarding behavior is present in all orders of Arachnida, but exclusive postzygotic paternal investment is restricted to members of the order Opiliones. Four cases have been recorded so far. Males of *Zygopachylus albomarginis* (Chamberlin 1925), a Manaosbiidae from Panama, build a cup-like nest on tree trunks made of mud and debris. During the breeding season the mud nests may be inspected by several females that occasionally lay 1-5 eggs. After oviposition, females leave the nests and the males remove fungi, chase potential predators away and prevent cannibalism (Rodriguez & Guerrero 1976; Mora 1990). In *Lepchana spinipalpis* Roewer 1927, an Assamiidae from Nepal and *Gonyleptes saprophilus* Mello-Leitão 1922, a Gonyleptidae from southeastern Brazil, males guard an egg-batch containing eggs in different developmental stages and even newly hatched nymphs (Martens 1993; Machado & Raimundo 2001). In these cases, possibly more than one female contributes to the batch at different times, as recorded for *Z. albomarginis*. In *Leytodoxis oviger* Martens 1993, a Podoctidae from the Philippines, females attach four or five eggs directly to the fourth femur of the males that carry the eggs until they hatch (Martens 1993).

Incipient cases of biparental care or an "alternative" form of paternal care were observed among goniosomatines, in which males are able to care for the brood when guarding females desert or die. Males of *Goniosoma longipes* (Roewer 1913)

(Gonyleptidae, Goniosomatinae) may defend a territory on a cave wall where females lay eggs and take care of their batches (Machado & Oliveira 1998). If a female is experimentally removed from her egg-batch, the male guards eggs for up to two weeks (Machado & Oliveira 1998). Similarly, in *G. albipunctum* Mello-Leitão 1932, whose females also regularly take care of the offspring, a male was once observed guarding eggs and nymphs in the field (Willemart & Gnaspini in press). Additionally, in *G. spelaeum* (Mello-Leitão 1923) several males were observed close to guarding females (Gnaspini 1995), suggesting that males could either defend his mate and/or occasionally defend the offspring. Machado & Raimundo (2001) suggest that the association between males and their offspring through the defense of an oviposition site may constitute the basis for the evolution of paternal care in most harvestmen species.

In this paper we report a new case of male egg guarding behavior in harvestmen. *Ampheres leucopheus* (Mello-Leitão 1922) belongs to the subfamily Caelopyginae (Gonyleptidae) and inhabits the rain forests of southern and southeastern Brazil. Behavioral observations were conducted in the laboratory on a guarding male captured at Parque Estadual Intervales (Ribeirão Grande, São Paulo State) in February 2000. The branch containing the egg-batch and the guarding male was taken to the laboratory to investigate if the parental individual

would also care for nymphs. The male and the egg-batch were maintained in a plastic box ($17 \times 13 \times 10$ cm) for three days until the hatching of the first nymphs, at around 25°C and relative humidity of 70–80%. Twenty-four hours after the hatching of the first nymphs, the male, juveniles and remaining eggs were preserved in 70% ethanol. Measurements of egg diameter were taken with calipers (0.01 mm) before preservation. To assess the fecundity of females, ten preserved individuals collected in localities near the study sites were dissected and the number of eggs in the reproductive tract was counted. The dissected individuals were deposited at Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo State, Brazil (numbers: HS 256, 6541, 14133, and 14199).

Field observations were conducted on three guarding males found near Guaricana Dam (São José dos Pinhais, Paraná State) in December 2001. The presence of these three guarding males near the eggs were checked four times during one afternoon (1300–1900 h), totaling 12 events of field observation. Each observation event lasted 5–10 min. Voucher specimens were deposited at Museu de Zoologia da Universidade de São Paulo and Museu de História Natural da Universidade Estadual de Campinas (ZUEC), São Paulo State, Brazil.

Egg-batches were laid on the underside surface of leaves, attached by a very abundant transparent mucous layer (Fig. 1). The three egg-batches observed directly in the field contained more than 100 eggs (165 eggs in Fig. 1; eggs of the other two were not counted), and the one taken to the laboratory contained 216 eggs. Like many laniatorean harvestmen (Gnaspini 1995; Machado & Oliveira 1998), eggs of *A. leucopheus* darken during the embryonic development: recently laid eggs are white or yellowish, and just prior to hatching they are dark brown with many black spots. A curious pattern observed in all four egg-batches (see Fig. 1) is that older eggs were placed closer to the leaf apex, probably meaning that eggs are laid from the leaf apex towards its base, where the male rests. The average diameter of the eggs taken to the laboratory, measured just before hatching, was 1.42 mm ($\text{SD} = 0.10$ mm; range = 1.24–1.52; $n = 10$). From this egg-batch, 140 nymphs hatched within two days and the remaining 76 eggs were in an intermediate stage of development (based on the external coloration). Had the male been cannibalizing the eggs, we would expect a reduction in the number of eggs over time. Reduction in the number of eggs was observed neither in the field nor in the laboratory. In addition, the males were observed in a typical resting posture that was very similar to the posture of guarding females (see below), and not in their activity posture that would be needed if they were eating the eggs.

Of the ten dissected females, six contained eggs

in the reproductive tract. The number of mature eggs ranged from 20–36 ($\text{mean} \pm \text{SD} = 28.2 \pm 5.7$), much less than the total number of eggs found in each batch in the field. This pattern differs from several species presenting only maternal care, such as *Goniosoma longipes*, *Goniosoma* aff. *proximum*, *Neosadocus* sp. and *Discocyrtus oliverioi* H. Soares 1945, in which the number of eggs in the female reproductive tract is similar to that observed in batches found in the field (G. Machado unpub. data). This suggests that males accept eggs from more than one female or from the same female at different times. Although the second hypothesis seems to be unlikely, some guarding females of *Goniosoma* are known to copulate when guarding their eggs, and to add a few eggs to the batch during the brooding period (Gnaspini 1995; Machado & Oliveira 1998).

In eight out of the 12 field observations, males of *A. leucopheus* were seen resting near the eggs (Fig. 1), with no specific behavior toward the eggs, similar to the posture and behavior adopted by guarding females of several other harvestmen (see Gnaspini 1995; Machado & Oliveira 1998). In the remaining four events, however, the guarding males were not observed near the egg-batches. While one male was always seen close to the eggs, a second male was not seen near the eggs twice and a third male was not seen close to the eggs also twice. In one of these cases, the male was back to his guarding position in the following sampling event. In another case, the male was seen walking near the stem of the tree (ca. 20 cm from the leaf with his egg-batch) towards the canopy. It is possible that the males were guarding their batches at distance or even patrolling the surrounding area, as occurs in *Z. albomarginis* (Mora 1990). This behavior contrasts with that of egg-guarding females, which do not leave their egg-batches, even to forage (e.g., Gnaspini 1995; Machado & Oliveira 1998). However, in the laboratory, the male remained near the offspring even after the hatching of the first nymphs.

Although we have only a few observations and little is known about the reproductive biology of Caelopyginae, we suggest that the behavior observed in *A. leucopheus* is a case of exclusive paternal care. We suggest that the hypothesis of “alternative” paternal care, like that observed for some Goniosomatinae species (Machado & Oliveira 1998; Willemart & Gnaspini in press), is unlikely for *A. leucopheus*. If it was the case, we would expect to find some egg-batches guarded by females, but we observed none, even though the species was reproductively active.

Recently, Tallamy (2001) analyzed all described cases of exclusive paternal care in arthropods and suggested that male guarding behavior could release females from the fecundity constraints of maternal

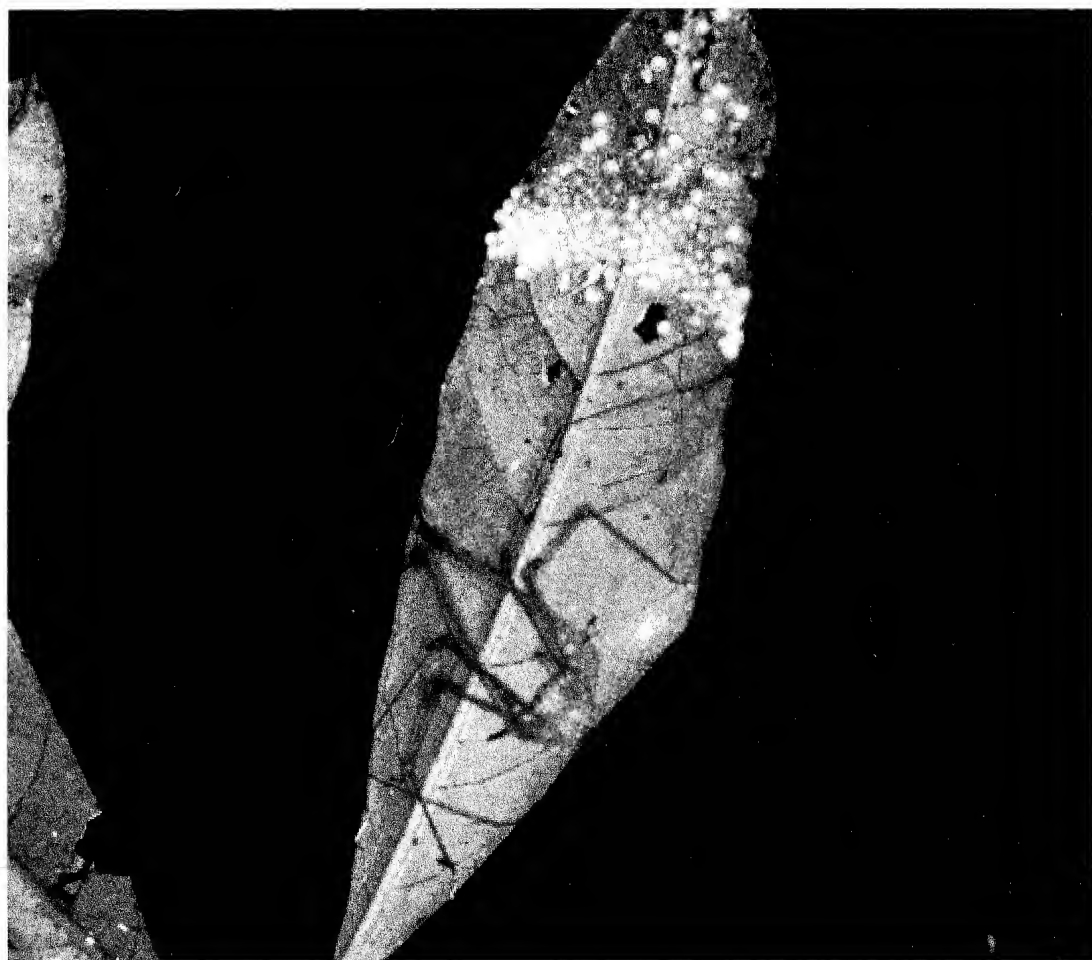


Figure 1.—Male of *Ampheres leucopheus* (body length = 1 cm) in resting position near eggs laid on the underside surface of a leaf in the forest near Guaricana Dam, São José dos Pinhais, Paraná State, Brazil.

care and provide an honest signal of paternal intent and quality. Therefore, males that are willing to take care of the offspring become preferred mates for females and may achieve a greater number of copulations than males that are unwilling or unable to care for eggs. The predictions of exclusive paternal care as a sexually-selected male trait are: (a) females are iteroparous; (b) there are many mating opportunities for the males; (c) care interferes with female foraging; (d) eggs increase male attractiveness; (e) males may guard eggs laid by several females; (f) males are willing to guard unrelated eggs and (g) the local female population is high (Tallamy 2001). At least *Z. albomarginis*, *L. spinipalpes* and *G. saprophilus* fit well to most of these predictions. For *A. leucopheus*, however, detailed observations in the field are needed to allow proper conclusions, but these preliminary results seem to corroborate a crucial point of Tallamy's hypothesis: males may

guard eggs from more than one female, as discussed before.

This is the second case of exclusive paternal care described for members of the large family Gonyleptidae (see Machado & Raimundo 2001). Because *G. saprophilus* belongs to the subfamily Gonyleptinae, which is not closely related to Caelopyginae (see Pinto-da-Rocha 2002), it is possible that paternal care in gonyleptid harvestmen evolved independently. In addition, "alternative" paternal care evolved in a third and unrelated subfamily, the Goniosomatinae. In the future, behavioral studies on other species of Gonyleptidae allied with the phylogenetic information (Pinto-da-Rocha 2002) could help to answer how many times paternal care has evolved within the family and if male guarding in harvestmen evolved from no care or from female care. Finally, it is possible that paternal care among harvestmen is more common than previously

thought, and that more cases will be detected when a larger number of species are studied, especially the tropical laniatoreans.

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SHORT COMMUNICATION

MATING WITHOUT SEXUAL CANNIBALISM IN *TIDARREN SISYPHOIDES* (ARANEAE, THERIDIIDAE)

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ABSTRACT. Copulatory behavior of *Tidarren sisypoides* is described for the first time. Courtship proceeds without construction of a mating thread. The male dies during insertion and remains coupled to the female epigynum for 2.4 hours on average ($n = 15$). In contrast to other species hitherto studied, females of *T. sisypoides* do not consume their mates after copulation. Instead, the dead males are removed from the webs by the females.

Keywords: One-palped spiders, copulatory behavior, male sexual suicide, mating plug

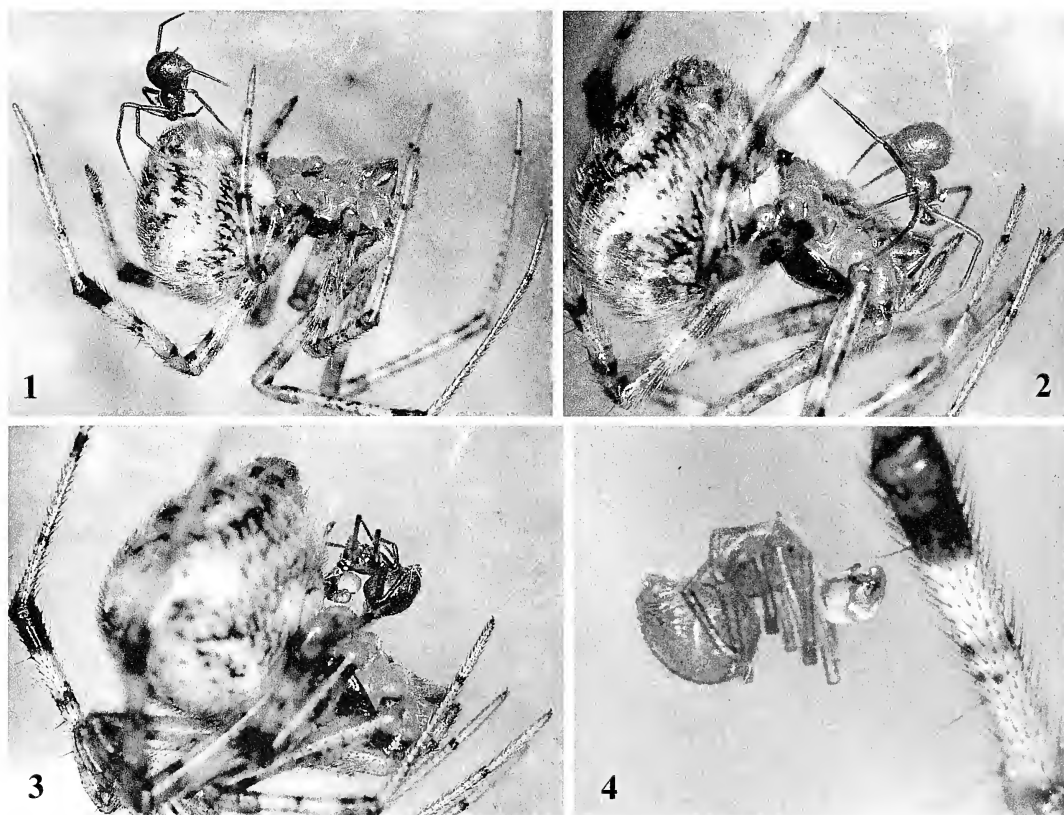
The spider genera with a single male palp, *Tidarren* and *Echinotheridion*, are famous for their peculiar morphology and behavior (Chamberlin & Ivie 1934; Branch 1942; Levi 1955; Schmidt 1980; Knoflach & van Harten 2000, 2001; Knoflach 2002). Males dislodge one of their palps by self-amputation shortly after the penultimate molt. Copulation involves a single palpal insertion and always results in the male's death. Sexual cannibalism occurs either after insertion, as in *Tidarren cuneolatum* (Tullgren 1910), or even during insertion by emasculation, as in *T. argo* Knoflach & van Harten 2001 and *Echinotheridion gibberosum* (Kulczynski 1899), and thus in all species hitherto studied (Knoflach & van Harten 2000, 2001; Knoflach 2002). However, as reported herein, the type species *Tidarren sisypoides* (Walckenaer 1841), which occurs from southern USA to South America, is different from the above species. Sexual size dimorphism is very pronounced in this species (Figs. 1–5).

Material examined: Descendants of one eggsac, Mexico, Chiapas state, Tapachula, Rosario Itzapa, 6.-12.10.2001, leg. S.P. Benjamin and J.A. Garcia-Ballinas. Males and females were reared to adulthood in captivity in Innsbruck. Fecundity is considerable in this species with several hundred eggs in an eggsac (Guarisco 2000). Depository: Voucher specimens (males and females) are deposited in the American Museum of Natural History, New York; California Academy of Sciences, San Francisco; Muséum d'Histoire naturelle, Genève; Muséum d'Histoire Naturelle, Paris; Naturhistorisches Museum Wien.

Postembryonic development: Males molt 3–4 times (incomplete stages within cocoon not taken into account) and mature c.55 days after hatching from the cocoon; females need 5–6 molts and c.100 days to reach maturity (Gonzalez 1982). The sub-adult stage of males reared from this Mexican eggsac lasted 11.6 days on average (± 0.54 s.e., range 10–18, $n = 18$).

Palp-amputation: Branch (1942) gives a detailed description of the palp-amputation of *T. sisypoides* [sub *T. fordum* (Keyserling 1884)]. A few hours after the penultimate molt, one palp is twisted off and thereafter sucked out by the male spider. One amputation took place 1h 40min after the molt and lasted only three minutes (pers. obs.).

Copulatory behavior: Altogether 15 copulations were observed. When introduced into the females' webs, males almost immediately became active ($\bar{x} = 0.9$ min, $n = 13$). Courtship was rather short, 1.6 min on average (± 0.26 s.e., range 0.3–3.7 min, $n = 13$) and females generally remained completely motionless. In one out of 15 cases the female vibrated her abdomen once. In contrast to other one-palped spiders, courtship proceeded without construction of a mating thread by the male. Distant courtship movements of the male, if performed at all, consisted of some walkabouts near the female, sometimes combined with irregular web-spinning behavior ($n = 3$) and/or jerks ($n = 2$). Only one male intensively shook his body. In seven cases, there were no distant courtship movements and direct contact courtship predominated. After contacting the female, the male palpated the female's hind legs or abdomen, mounted the female venter from



Figures 1–4.—Phases of copulatory behavior in *Tidarren sisypoides*. 1. Male mounting venter of female. 2. Contact courtship: male palpating sternum and mouthparts of female. 3. Copulation: male's legs already contracted. 4. Dead male removed from the epigynum after 'passive' insertion, not consumed by female. Note size of female's tibia IV for comparison.

behind (Fig. 1) and sometimes also moved forward to the female's sternum, throughout palpating her body and her hindlegs with his legs (Fig. 2). In response to these movements, the female lowered her body. This apparently represented the copulatory posture.

To achieve insertion, the male approached the epigynum from behind. Each insertion succeeded at once on the first attempt. The large modified cymbium was put over the epigynal protuberance and was immediately fixed. At the beginning of copulation the male's legs were stretched straight out. After approximately three minutes his legs became contracted, which evidently indicated the male's death (Figs. 3, 5). He remained passively coupled to the female, while she was cataleptic. There were no obvious movements by either partner. Duration of copulation was highly variable, ranging from 14–380 minutes and lasting on average $146 (\pm 36.7 \text{ s.e.}; n = 15)$ minutes. Finally, the female removed the dead male from the epigynum and cast him away without cannibalizing him ($n = 15$). His palp remained inflated (Fig. 4). Copulatory scars, which

were presumably produced from copulation by piercing the posterior epigastric region in *Echinothridion cartum* Levi 1963 (Ramirez & Gonzalez 1999), have not been found in *T. sisypoides*.

Multiple mating: Copulations with a second male were similar to first copulations. This is to be expected, as one receptacle still is virgin after the first copulation (see Knoflach & van Harten 2000). Two females were allowed to copulate a third time. In one case, the third male inserted his palp as usual, but was removed by the female after just three minutes. Prior to this insertion the female vibrated her abdomen and moved her legs II up and down. Both movements are reminiscent of typical courtship elements of other *Tidarren* females (Knoflach & van Harten 2000, 2001). No copulation took place with the second female. The male immediately mounted the female's venter, but the female was restless. The male calmed her by climbing forward to her mouthparts and back again, always palpating her. Finally, his mouthparts touched her epigastric furrow and his palp touched her epigynum without being inserted. After three minutes of such contact the fe-

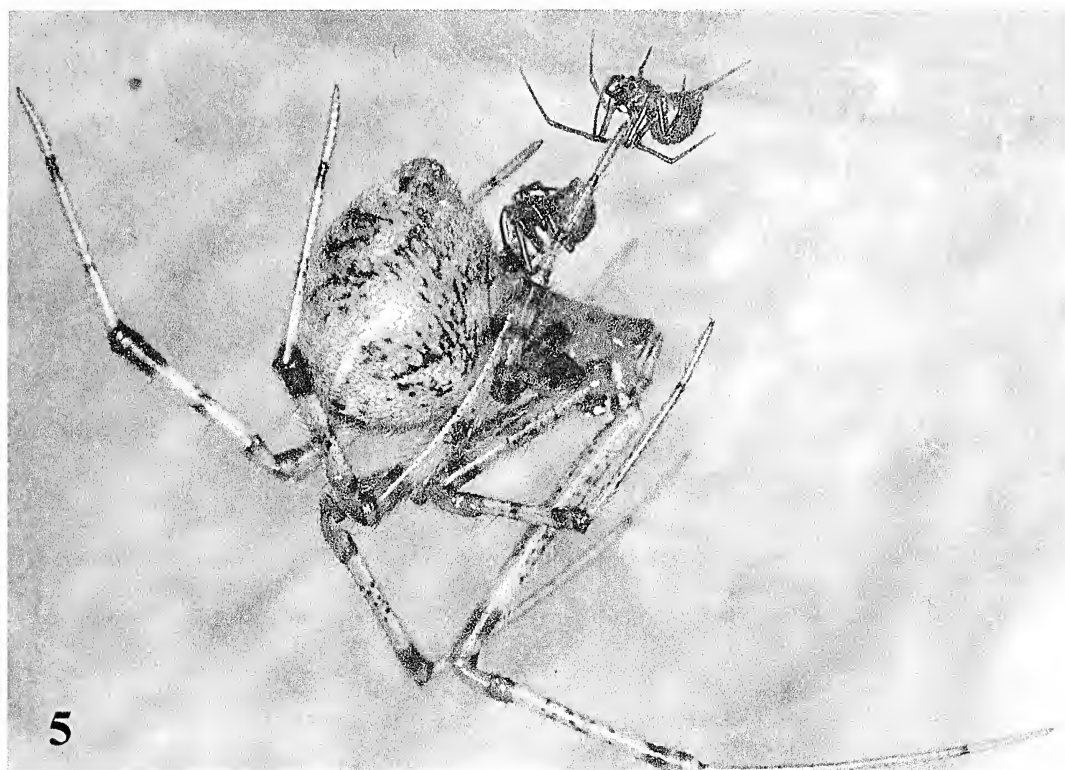


Figure 5.—Copulation in *Tidarren sisypoides*. Approach of second male, which was the successive mate.

male pulled him off with her hindlegs. The male again approached after one minute, mounted her and repeated contact courtship as described above. Again his mouthparts were positioned on her epigastric furrow, as if he was ingesting fluid. He was again pushed away and then left her web. Although the sample size was small, it should be noted that both females were unusually active, no longer cataleptic.

The sudden death of males appears to coincide with copulation in all one-palped spiders. In *T. sisypoides* the male's legs become contracted after three minutes. Emasculation, amputation of the male palp by the female, as known for *T. argo* and *E. gibberosum* (Knoflach 2001; Knoflach & van Harten 2000, 2001) and perhaps to be assumed also for *E. cartum* (see Ramirez & Gonzalez 1999), is not present in *T. sisypoides*. Instead of the separated male palp, the entire male body of *T. sisypoides* may serve as a temporary mating plug, lasting 2.4 hours on average. The moment of removal is determined by the female. She may pull off the male in as little as 14 minutes or after more than six hours. Interestingly, sexual cannibalism does not take place in *T. sisypoides*, although females preyed upon insects, which were similar in size than the males. This also confirms that absence

of predation on males was not because females were satiated. Copulation of *T. sisypoides* differs from the other known one-palped spiders by the following: no mating thread is constructed, female courtship is not discernible and sexual cannibalism does not occur. Have all these elements been secondarily lost in this species? As sexual size dimorphism is much larger in *T. sisypoides* than in the other species, consumption of the dead male may therefore have been reduced in this species. A better understanding of the phylogeny of the species of *Tidarren* and *Echinotheridion* will probably help to elucidate the evolution of these behaviors.

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Figures 27–34. — Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

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